THE GUNONG BENOM EXPEDITION 1967

13. NOTES ON ZOOGEOGRAPHY, CONVERGENT EVOLUTION AND TAXONOMY OF FLEAS (SIPHONAPTERA), BASED ON COLLECTIONS FROM GUNONG BENOM AND ELSEWHERE IN SOUTH-EAST ASIA
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BY
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CONTENTS

SYNOPSIS

The Siphonapteran genus *Medwayella*, like other pygiopsyllids, is believed to have descended from fleas originating in the Australian Region, but it is a comparatively youthful taxon, with its centre of development in Borneo. Throughout its range, which is primarily in the Malayan Subregion, it is especially associated with callosciurine squirrels in the foothills and lower mountains. Other Oriental squirrel-fleas are of definite Palaearctic affinity, as are those of the insectivores and as is true for certain local murid-fleas. The data on Siphonaptera suggest that the squirrels and insectivores occurring in what is here termed the Insular Malayan Area, had their origin on the Asian Mainland. The route of entry to Borneo, however, seems to have been from Malaya through Sumatra or Java, rather than across the China Sea from Indo-China to northern Borneo. It is also clear that some members of the genus *Rattus*, and especially the subgenus *Rattus*, through the eons, must have moved back and forth between the Malayan Peninsula and Indonesia and Borneo, etc., since some of their fleas are of definite Palaearctic ancestry, and indeed one such genus occurs as far east as New Guinea. These rats, along with their fleas of Asian descent, are presumed to be recent entries, geologically speaking. However, the fleas of the more ancient rats in New Guinea and the so-called 'Malfilindo Archipelagoes' are all pygiopsyllids and are believed to have had their roots in the Australian Region, and the forebears of these murids themselves may have originated there as well.

Malaya, Sumatra, Java and Borneo share many faunal features, although the Javanese fauna is relatively impoverished, while the mammals and fleas of Sarawak resemble those of Malaya more closely than do those of Sabah. Palawan seems to have obtained its squirrels and tree-shrews and some rats and related fleas from northeast Borneo, while much of the Mindanao fauna apparently entered from southeastern Sabah. Mindanao, however, also has faunal elements from Celebes and the New Guinean Subregion. The data also provide support for the theory of Continental Drift in suggesting that there were ancient faunal connections, involving 'island-hopping' mammals and their fleas, between the Southern Continents.

I. INTRODUCTION

Study of the distribution and hosts of the genera of Siphonaptera treated in the first article in this series not only contributes to our understanding of the zoogeography of fleas and of their hosts, particularly as pertains to Southeast Asia and the

islands of the Oriental Region, but also appears to be of significance in subjects as far afield as the theory of Continental Drift (Traub, in prep.) and medical geography (Traub et al., in prep.). Accordingly, an analysis of the geographic and host relations is herewith presented in some detail, along lines listed in the Table of Contents, and the data suggest that the forebears of *Medwayella* Traub, 1972, and other pygiopsyllids originated in the Australian Region or Wallacea, not the Asian mainland, but that other Oriental squirrel-fleas (and the squirrels) and the non-pygiopsyllid fleas of the subgenus *Rattus* Fischer, 1803, were derived from Palaearctic stocks. The data also indicate that Java has had a different faunal history than has Sumatra, and that the rodents and fleas of Sarawak have significantly more in common with Malaya than do those of North Borneo (Sabah). Evidence suggesting that there were tenuous, aboriginal faunal connections between the southern continents, as by 'island-hopping' mammals, is mentioned only briefly and occasionally, since the subject of Continental Drift will be treated in detail elsewhere (Traub, in prep.).

In order to facilitate the discussion, much of the basic data and observations on pertinent Siphonaptera and their hosts are presented first, in a special section which includes a review of squirrel-fleas from various parts of the world. Generalizations and deductions based upon such material are presented in the subsequent section on Discussion, where highlights of the data are reviewed, and where new information (citing sources) is given as required. The section on Conclusions summarizes the results.

In general, the Zoogeographic Regions and Subregions cited here are those used by Bartholomew, Clarke & Grimshaw (1911), but with certain new qualifications regarding Subregions, based upon unpublished notes (Traub & Hoogstraal, in litt.). Thus, it has been recognized that a map-reading alone is insufficient for denoting the limits of a Subregion, since the ecology of a particular area, depending upon the altitude or rainfall, may be an over-riding factor. Hopkins & Rothschild (1966) therefore refer to 'the occurrence of "islands" which belong faunistically to one region in a "sea" of another' and cite, as an example, the fact that the mountains of Guatemala and southern Mexico evidently have a Nearctic flea-fauna though that of the lowlands at their foot is Neotropical. In the present article, this concept has been extended. Thus, the *mesic* elements of the Himalayas and adjacent mountains, and the mountains of Formosa (Taiwan) are deemed as being in the 'Eastern Palaearctic Subregion'. Instead of being placed in the Oriental Region as heretofore, the *xeric* parts of western Pakistan and India, etc., are here considered as being in the 'Southeastern Palaearctic Subregion' (along with the arid side of the Himalayas), since their faunal affinities are with the deserts of Soviet Central Asia and Iran. The Oriental Region is herein divided into the following Subregions: (1) The Indian Subregion, as used in this paper, is limited to the plains and monsoon areas of the subcontinent, western Burma, Ceylon, the terai of Nepal, etc. (2) What is here termed the 'Burmo-Chinese Subregion' encompasses not only the continent from Assam east to Indo-China, but south to northern Malaya, and including the foothills and lowlands of Formosa. (3) The 'Malayan Subregion' as used here includes Malaya south of Perlis, Borneo, Sumatra, Java, Bali and Palawan (Philippines). The other islands of the Philippines are a zoogeographic problem and have

been assigned to various Subregions (Darlington, 1963) or ignored. Tentatively, I am placing Luzon in the Southeastern Oriental Subregion, and the remaining islands in the Malayan Subregion. Unpublished data suggest that Mindanao has some faunal similarities with Celebes, which is here placed in the 'Wallacean Subregion' (Wallacean Region) along with Timor and the Lesser Sundas. It is impossible for me to evaluate such observations without adequate information about the Siphonaptera and mammals of the lowlands, foothills and mountains of Mindanao and of Celebes. The Moluccas, Ceram, etc., are placed in the Moluccan Subregion, but we have no data on Siphonaptera from those islands.

In accordance with this concept of using ecological factors and faunal affinities in denoting zoogeographical areas, the Nearctic Region is regarded as extending along the upper regions of the mountain ranges into northern South America. These montane areas commencing south of the deserts of northern Mexico are termed the 'Temperate Middle American Subregion', while the Neotropical Region is viewed as extending north along the coasts of Mexico.

From the geographic or cartographic point of view this system has drawbacks. Thus, it is awkward to have the Oriental Region rent by the vast mountain-ranges of the Himalayan Chain, so that, for example, much of Burma and south Yunnan are both in the Oriental Region, but between them are massive Palaearctic 'islands' of the Himalayas. However, faunistically and geologically, this makes sense. The Himalayas are actually a young group of mountains, and it appears that the tremendous ecological changes wrought by the relatively recent upthrusts (e.g. creation of deserts in the rain-shadows) have obliterated or drastically modified florae and faunae that formerly were distributed continuously across much of southern Asia. As a result, despite the extensive patches of desert, there exist 'ecological islands' scattered amongst the mountains throughout the region, where these same groups of mammals, ectoparasites, associated microbial infections and plant-habitats may be found as relics of past eons (Traub & Evans, 1967; Traub & Wisseman, 1968).

Allusion was made, in the first article in this series, to the difficulties posed by the multiple meanings ascribed to geographical names, especially when the terms acquire political connotations which vary with the passage of time. Good (1964), for example, referred to the confusion associated with the name Malaya and its allied forms, and therefore defined and limited such usage in his opus (p. 20) as follows: (1) Malay Peninsula—'that part of continental Asia south of the isthmus of Kra'; (2) Malayan Archipelago—'the islands thence as far as and including New Guinea' and (3) Malaysia—'both together'. This is a useful terminology, but the current use of the name Malaysia to denote the countries of Malaya and the former British colonies in Borneo has added a new source of confusion. Also, in zoogeography, apparently in contrast to plant-geography, it is desirable to deal with New Guinea and adjacent islands as an entity rather than something submerged in a 'Malayan Archipelago'. A different terminology is required, and valid objections can be, and have been, raised to all proposals. Nevertheless, for purposes of convenience, utility and uniformity, it seems desirable to select and specify names for the main geographic areas used in this paper. Accordingly, in addition to the

Regions and Subregions as defined above, and the standard names of countries and islands, etc., the following are employed: (1) 'Malayan Peninsula' for the continental area south of the Isthmus of Kra. (2) The acronym 'Malfilindo Archipelagoes' for the entire groups of islands of Indonesia, Philippines and Borneo but excluding the islands of the New Guinean Subregion. (3) 'Southeast Asian Mainland' for the entire continental land-mass encompassed in the Oriental Region with the exclusion of the Indian Subregion. The Palaearctic portions of the Himalayas are therefore included. (4) The 'Oriental Mainland of Southeast Asia' refers to that same area in the zoogeographic sense, i.e. limited purely to the Oriental aspects and therefore excluding the Himalayas. (5) 'Insular Malayan Area' for the islands of the Malayan Subregion, i.e. Borneo, Java, Sumatra and the Philippines (excluding Luzon). (6) Australo-Asian Archipelagoes for the entire group of islands, from Sumatra and the Philippines to, and including, New Guinea and Australia.

Two other points are mentioned for clarification and emphasis. Throughout, the term 'Oriental' has a zoogeographic connotation, meaning the Oriental Region, and it is *not* used in the geographic, political, ethnological or popular sense denoting China and Japan. Secondly, unless otherwise indicated, all comments about numbers of taxa of Siphonaptera refer to the fleas of non-volant hosts only, and not necessarily to all the known genera or species. This approach is desirable in zoogeography because bats and birds may fly enormous distances, and the fleas found on them in one area may really be more representative of another, having accompanied the host on its journey.

The sources for the scheme of taxonomy and nomenclature of mammals are presented near the end of the article (p. 443), but scientific references are cited when unusual or controversial names are used.

The data presented below, in essence, include all the known fleas from Malaya, Sarawak, Sabah, Thailand, Indo-China, the Philippines, etc., with the exception of commensal species, bat-fleas and bird-fleas.

II. DATA AND OBSERVATIONS

A. Distribution of Relevant Mammals in Pertinent Areas

1. Introduction

In discussing the zoogeography of fleas, it is necessary to consider that of the hosts, and accordingly data are first presented on the distribution of the major hosts for which we have records on mammal-fleas, in the Burmo-Chinese and Malayan Subregions of the Oriental Region. Data on Siphonaptera will be presented thereafter.

It should be borne in mind that no effort is made to treat all the rats and squirrels that occur within the geographical areas cited, since in some important instances data on Siphonaptera are lacking. Even with these limitations, however, certain generalizations appear warranted and zoogeographic trends can be noted which appear valid, as will be shown later.

Members of the sciurid tribe Callosciurini of the subfamily Sciurinae are particularly well represented in the Malayan and Burmo-Chinese Subregions, and since these tree-squirrels and 'ground-squirrels' have a relatively rich Siphonapteran

fauna, and apparently constitute the main hosts of the genus *Medwayella*, they are treated in some detail. The Petauristinae, or flying-squirrels, are also wealthy in numbers of genera and species in this Subregion, certainly far more so than in the Palaearctic and Nearctic Regions. However, since relatively little is yet known about the fleas of Oriental flying-squirrels, these mammals are not included in the charts listing geographic areas, and are mentioned only briefly throughout.

2. Squirrels and Murids Occurring in Malaya and Borneo

Malaya and Borneo have a rich fauna of murids and squirrels, especially callosciurines, both as genera and as species, as indicated in Table 1. It is noteworthy that a significant number of the genera, and even the species, are found in both areas. Thus, Malaya and Borneo share 6 of 12 genera of squirrels and 3 of 7 murids, while 9 out of 25 species of squirrels, and 12 of 30 non-commensal species of murids are found in both areas. Further, some of the species treated as distinctive are actually closely allied, so that, for example, the Malayan *Rattus* (*Stenomys*) *bowersi* (Anderson, 1879) may be regarded as a sibling species of the Bornean *R.* (*S.*) *infraluteus* (Thomas, 1888) (just as their respective fleas are siblings), and the Malayan *R.* (*Lenothrix*) *inas* Bonhote, 1906, deemed the twin species of Bornean *R.* (*L.*) *alticola* (Thomas, 1888). However, it is also pointed out that Borneo exhibits an important degree of endemicity, especially with respect to sciurids. Thus, *Rheithrosciurus* Gray, 1867, and *Glyphotes* Thomas, 1898, are found nowhere else, while *Exilisciurus* Moore, 1958, is known elsewhere only from the Philippines, and *Nannosciurus* Trouessart, 1880, from Java and Sumatra. *Haeromys* Thomas, 1911, occurs only in Celebes and Borneo. The Malayan taxa not listed for Borneo are generally northern forms reaching the limit of their ranges in Malaya (e.g. *Hapalomys* Blyth, 1859, *Bandicota* Gray, 1873, and *Menctes* Thomas, 1908), or else are restricted to Malaya, Sumatra and Java, such as *Pithecheir* Cuvier, 1838.

Of particular relevance is the distribution of non-commensal murids and squirrels within Borneo, especially insofar as concerns Malayan species, and this is treated in Table 2. (Since little is known about the fleas of Indonesian Borneo or Brunei, those regions are not considered herein.) Of the mammals listed, 10 of the murids and 7 of the squirrels are found in all 3 areas. Six of the rats and 9 of the squirrels are absent from Malaya. Three of the rodents are limited to Malaya and Sarawak, viz., *Rattus* (*Lenothrix*) *canus* (Miller, 1903), *Lariscus* (*L.*) *insignis* (F. Cuvier, 1821) and *Sundasciurus* (*S.*) *tenuis* (Horsfield, 1824). Of the Bornean rats, 3 are found only in North Borneo (Sabah), and there is 1 species of squirrel which is known only from Sarawak. *Glyphotes* (*G.*) *simus* Thomas, 1898 and *Lariscus* (*Paralariscus*) *hosei* (Thomas, 1892) are reported only from northern Sarawak and from Sabah, while *Rheithrosciurus macrotus* (Gray, 1856) apparently does not occur farther north than the south of Sabah.

It therefore appears that there are rather significant faunal differences between Sabah and Sarawak, even though a large proportion of these rodents occur in both areas, and even Malaya as well. It is noteworthy that none of the rodents common to both Sabah and Malaya are absent from Sarawak, suggesting that the path of migration was via Sarawak.

Table 1

Species of squirrels (excluding flying-squirrels) and murids occuring in Malaya and Borneo

Murids	Malaya	Borneo
Bandicota bengalensis	+	
Bandicota indica	+	
Chiropodomys gliroides	+	+
Chiropodomys major		+
Chiropodomys muroides		+
Haeromys margarettae		+
Haeromys pusillus		+
Hapalomys longicaudatus	+	
Mus musculus	+	+
Pithecheir melanurus	+	
Rattus (Leno.) alticola		+
Rattus (Leno.) baeodon		+
Rattus (Leno.) canus	+	+
Rattus (Leno.) inas	+	
Rattus (Leno.) ochraceiventer		+
Rattus (Leno.) rajah	+	+
Rattus (Leno.) surifer	+	+
Rattus (Leno.) whiteheadi	+	+
Rattus (Leop.) edwardsi	+	
Rattus (Leop.) sabanus	+	+
Rattus (Maxomys) cremoriventer	+	+
Rattus (Maxomys) fulvescens	+	+
Rattus (Maxomys) niviventer	+	
Rattus (Rattus) annandalei	+	
Rattus (Rattus) argentiventer	+	+
Rattus (Rattus) baluensis		+
Rattus (Rattus) exulans	+	+
Rattus (Rattus) norvegicus	+	+
Rattus (Rattus) rattus	+	+
Rattus (Rattus) tiomanicus	+	+
Rattus (Stenomys) bowersi	+	
Rattus (Stenomys) infraluteus		+
Rattus (Stenomys) muelleri	+	+

Squirrels	Malaya	Borneo
Callosciurus albescens		+
Callosciurus caniceps	+	
Callosciurus erythraeus	+	
Callosciurus nigrovittatus	+	+
Callosciurus notatus	+	+
Callosciurus prevosti	+	+
Dremomys everetti		+
Dremomys rufigenis	+	
Exilisciurus exilis		+
Exilisciurus whiteheadi		+
Glyphotes (G.) simus		+
Glyphotes (Hess.) canalvus		+
Lariscus (L.) insignis	+	+
Lariscus (Para.) hosei		+
Menetes berdmorei	+	
Nannosciurus melanotis		+
Ratufa affinis	+	+
Rheithrosciurus macrotis		+
Rhinosciurus laticaudatus	+	+
Sundasciurus (Alte.) hippurus	+	+
Sundasciurus (S.) brookei		+
Sundasciurus (S.) jentinki		+
Sundasciurus (S.) lowi	+	+
Sundasciurus (S.) tenuis	+	+
Tamiops macclellandi	+	

Summary—Numbers of taxa

I. Genera	Squirrels	Murids
Total	12	7
Number in common	6	3
Absent from Malaya	4	1
Absent from Borneo	2	3

II. Species	Squirrels	Murids
Total	25	33
Number commensal	0	3
No. of others in common	9	12
Absent from Malaya	11	9
Absent from Borneo	5	9

TABLE 2

Occurrence in Sarawak, Sabah and Malaya of certain squirrels and murids

Murids	Malaya	Sarawak	Sabah
Chiropodomys gliroides	+	+	+
Haeromys margarettae		+	+
Rattus (Leno.) alticola			+
		+	
Rattus (Leno.) baeodon		(North)	
Rattus (Leno.) canus	+	+	
Rattus (Leno.) ochraceiventer		+	+
Rattus (Leno.) rajah	+	+	+
Rattus (Leno.) surifer	+	+	+
Rattus (Leno.) whiteheadi	+	+	+
Rattus (Leop.) sabanus	+	+	+
Rattus (Maxomys) cremoriventer	+	+	+
Rattus (Maxomys) fulvescens	+	+	+
Rattus (Rattus) argentiventer	+	+	+
Rattus (Rattus) baluensis			+
Rattus (Rattus) tiomanicus	+	+	+
Rattus (Stenomys) infraluteus			+
Rattus (Stenomys) muelleri	+	+	+

Squirrels	Malaya	Sarawak	Sabah
Callosciurus albescens		+	+
Callosciurus nigrovittatus	+	+	+
Callosciurus notatus	+	+	+
Callosciurus prevosti	+	+	+
Dremomys everetti		+	+
Exilisciurus (2 species)		+	+
		+	
Glyphotes (G.) simus		(North)	+
Glyphotes (Hess.) canalvus		+	
Lariscus (L.) insignis	+	+	
		+	
Lariscus (Para.) hosei		(North)	+
Nannosciurus melanotis		+	
Ratufa affinis	+	+	+
			+
Rheithrosciurus macrotis		+	(South)
Rhinosciurus laticaudatus	+	+	+
Sundasciurus (Alte.) hippurus	+	+	+
Sundasciurus (S.) brookei		+	+
Sundasciurus (S.) jentinki		+	+
Sundasciurus (S.) lowi	+	+	+
Sundasciurus (S.) tenuis	+	+	

3. Tree-Shrews (Tupaiidae)

The group of mammals whose over-all distribution corresponds most closely to that of fleas of the genus *Medwayella* is that of the tupaiids, and hence these merit discussion. The classification of tupaiids is in rather confused state at both the ordinal level and that of the species. The tree-shrews are regarded as menotyphlous insectivores by Anderson & Jones (1967) but as lemuroid primates by Simpson (1945), Walker et al. (1968) and Morris (1965). The family was reviewed by Lyon (1913), but many of his 'species' are no longer recognized as such, if at all, and there has been no subsequent single work dealing with the distribution of tupaiids. Instead, mammalogists working with certain geographical areas have at times cited the relevant species, and even here a variety of names have been used for a single species. Table 3 lists the species of tupaiids occurring in specified regions, and presumably the only member of the family not cited is *Tupaia nicobaria* (Zelebor, 1869), of the Nicobar Islands. In compiling the list, Ellerman & Morrison-Scott (1951) was used as the authority for the range of *T. glis* (Diard, 1820) and *T. minor* Günther, 1876; Morris (1965) for tupaiids from Sumatra and Java; Medway (1963) for Borneo; Harrison (1964) for Malaya, and Taylor (1934) for *Urogale* Mearns, 1905.

It is apparent that the contemporary range of the family is wholly in the Oriental Region, from India to Palawan and Mindanao in the Philippines. Only 1 species, of a distinctive endemic genus, occurs in India and only 1 species (*Dendrogale murina* (Schlegel & Müller, 1845)) is found in Indo-China, while the second species of *Dendrogale* Gray, 1848, is restricted to Borneo. The monotypic *Urogale* is endemic to the Philippines (Mindanao). *Tupaia* Raffles, 1821, has the broadest range and the largest number of species, and its height of development seems to have been in Borneo, with 8 species listed for Sarawak and 5 of these occurring in North Borneo. Two of the Bornean species, *T. glis* and *T. minor*, occur in Malaya, and the former ranges from Assam to Palawan. It is of interest that 2 tupaiids (the monotypic *Ptilocercus* Gray, 1848, and *T. minor*) which are found in Sumatra, Malaya and Borneo, are absent from Java.

4. Additional Data on Mammals

Some of the tables which deal with the distribution of Siphonaptera, viz., Tables 6 and 7, also present data on relevant mammalian hosts, particularly insofar as concerns other areas of the Oriental Region. Thus, squirrels are treated in Table 6 (facing p. 404), whence it can be seen that certain species, such as *Tamiops macclellandi* (Horsfield, 1839) and *Menetes berdmorei* (Blyth, 1849), have a more northern or continental type of distribution, being found in Indo-China, Thailand and Malaya, but not Indonesia or Borneo, etc. *Callosciurus caniceps* Gray, 1842, is also in this category, but it occurs in Formosa (Taiwan) as well. The genus *Dremomys* Heude, 1898, as a whole, is wide-ranging in the Region, extending beyond some of the extremes of the Table, since it is also present in Nepal, south China, Assam, Burma and even Formosa. It is not known from the Philippines.

Most of the pertinent species of *Callosciurus* Gray, 1867, have a rather southern and eastern distribution—Malaya, Indonesia and Borneo, with *C. prevosti* Desmarest, 1822, and *C. notatus* Boddaert, 1785, reaching Celebes, and members of the

TABLE 3

Distribution of genera and species of tupaiids (primates, Tupaiidae) in specified areas

Genus and total number of species	South India	Assam or Burma	South China	Thailand	Indo-China	Malaya	Sumatra	Java	Borneo Sarawak	Borneo Sabah	Philippines Palawan	Philippines Mindanao
Anathana (1)	*ellioti*											
Dendrogale (2)					*murina*				*melanura*	*melanura*		
Ptilocercus (1)						*lowi*	*lowi*		*lowi*	*lowi*		
Urogale (1)												*everetti*
Tupaia (10) (?)		*glis*	*glis*	*glis* *minor*	*glis*	*glis* *minor*	*glis* *minor* *javanica* *tana*	*glis* *javanica*	*glis* *minor* *dorsalis* *tana* *gracilis* *montana* *picta* *splendidula*	*glis* *minor* *dorsalis* *tana* *gracilis* *montana*	*glis*	

C. hippurus-group (but not *C. hippurus* Geoffroy, 1832 *pcrse*) occurring on Palawan and Mindanao. (*Nannosciurus melanotis* (Müller, 1838) is found in Borneo, Sumatra and Java, and other *Nannosciurus* are present in Mindanao and a few other islands of the Philippines. The related *Exilisciurus exilis* (Müller, 1838) is known from Borneo and Sumatra.) All of the squirrels listed for Sumatra occur in both Malaya and Sarawak, but the converse is not quite true, for *Dremomys* has apparently not been reported from Sumatra. Of the 8 entries for squirrels from Sumatra, Malaya and Borneo, 4 are presumably absent from Java (*C. prevosti*, *C. hippurus*, *Sundasciurus* Moore, 1958, and *Rhinosciurus* Gray, 1843). It should be noted that no squirrels (nor tupaiids) have ever been reported from Luzon, and that sciurids are unknown east of the vicinity of Celebes.

There are 8 groups or species of rats listed in Table 7 (facing p. 406), and only 1 of these, *Rattus* (*Stenomys*) *bowersi*, is wholly continental Asian, but as mentioned, a closely related species, *R.* (*S.*) *infraluteus*, is endemic to Sabah. The broadest range is exhibited by *R.* (*Maxomys*) *fulvescens* (Gray, 1847), which actually is found as far north and west as Nepal and Tibet, and south and east all the way to Sabah. *R.* (*Lenothrix*) *rajah* (Thomas, 1894) and *R.* (*L.*) *surifer* (Miller, 1900) have often been misidentified or confused by mammalogists, at least until recently, and hence the 2 are regarded as a 'group' herein, occurring from Thailand to Palawan. Of the 3 species of rats listed as occurring in Malaya, Sumatra and Sarawak, one, *R.* (*L.*) *whiteheadi* (Thomas, 1894) is absent from Java.

Two insectivores are treated herein, *Hylomys suillus* Müller, 1839, the lesser gymnure, an erinaceid, which is found in all the areas cited save the Philippines, and *Crocidura* Wagler, 1832, species of which exist in all these countries, and many others in Asia and in Africa, etc.

B. Data on Distribution or Hosts of Siphonaptera

1. Pygiopsyllids in General

Inasmuch as *Medwayella*, *Lentistivalius* Traub, 1972 and *Stivalius* (s. str.) Jordan & Rothschild, 1922, are all pygiopsyllids, it is advisable to first make some generalizations about the distribution of that family of fleas, including material from the wealth of yet undescribed taxa at hand. Of the total of 33 genera (or species-groups) of pygiopsyllids of non-volant hosts known to me, 21 (63%) are found in New Guinea or Australia or both (Traub, in prep.). An additional genus of the Australian Region (*Pygiopsylla* Rothschild, 1906) is also known from Borneo. A total of 121 of 176 species (69%) of pygiopsyllids of such hosts are found in Australia or New Guinea. Seven genera occur in Indonesia or Borneo, and 5 in the Philippines. There is only 1 in the Palaearctic Region represented by a Japanese species of *Lentistivalius*, a wide-ranging genus known by a single species in Borneo (on tree-shrews), Malaya (on birds), Indian subcontinent (on shrews[1]) and in the Ethiopian Region of Africa (on rodents) (Traub, 1972a). There is now at hand a new species of murid-*Lentistivalius* from the Philippines. There is also an endemic African genus of 14 species,

[1] *L. ferinus* (Rothschild, 1908) ranges to Nepal, where it may possibly enter the fringe of the Palaearctic Region.

TABLE 4

Distribution of some† genera and species-group of pygiopsyllid fleas known from the Oriental Region and Wallacea

	Medwayella	*Stivalius* (s. str.)	*Gryphopsylla*	*jacobsoni*-group	*mjoebergi*-group	*pomerantzi*-group	New genus	*celebensis*-group	*Pygiopsylla*
Yunnan and South China		1			1*				
Indo-China	2* (1)				1*				
Thailand	3^{3}*				1*				
Malaya	6^{3}* (1)			1*	1*				
Sumatra	3*			1*					
Java	3^{2}*	1*		1*					
Celebes								1	
Borneo	11^{3}* (4)		1	(1)*	1				1
Philippines	(2)	1*		(1)*		2	1		
Indian Subcont.		3							
Total No. Spp. 21		5	1	2	2	2	1	1	1

* = One species occurs in more than one area.
New species are in ( ).
† = *Lentistivalius* is far-ranging and hence treated in the text.

Genus
Medwayella (21 spp.)
(Totals)
Macrostylopl (28 spp.)
(Totals)
Syngenopsyll (3 spp.)
(Totals)
Paraceras (10 spp.)†
(Totals)

Names in p
* = One ne
† = Includ
was from 'tro

TABLE 5

Distribution of species of genera of fleas which have representatives infesting squirrels in the Malayan and Southeastern Oriental Subregions

Genus	Himalayan or North Burma	South China Mountains	Ceylon	Taiwan	North Asia or Europe	Indo-China	Thailand	Malaya	Sumatra	Java	Borneo Sarawak	Borneo Sabah	Philippines Mindanao	Philippines Palawan
Medwayella (21 spp.)						*thurmani*	*robinsoni* *thurmani* *phangi*	*robinsoni* *phangi* *calcarata* *dryadosa*	*robinsoni*	*robinsoni* *dryadosa*	*robinsoni* *phangi* *calcarata* *veruta* *batibacula* *loncha* *rhaeba*	*veruta*		
						1 n. sp.		*limi* 1 n. sp.	*arcuata* *angustata*	*javana*		4 n. spp.	1 n. sp.	1 n. sp.
(Totals)						(2)	(3)	(6)	(3)	(3)	(6)	(5)	(1)	(1)
Macrostylophora (28 spp.)	*hastata*					*hastata*	*hastata*	*hastata* *levis*	*levis*					
		euteles *liae*		*liae*			*eutcles*							
	fimbriata *lupata* *uncinalis* *heinrichi*	*exilia* *trispinosa* *cuiae*	*phillipsi*			*pilata* *probata*			*idoneus* *sodalis*			*borneensis*		
				1 n. sp.*		1 n. sp.				2 n. spp.		3 n. spp.*	5 n. spp.	1 n. sp.
(Totals)	(5)	(5)	(1)	(2)		(4)	(2)	(2)	(3)	(2)		(4)	(5)	(1)
Syngenopsyllus (3 spp.)							*calceatus*	*calceatus*	*calceatus*	*calceatus*				
						1 n. sp.		1 n. sp.						
(Totals)						(1)	(1)	(2)	(1)	(1)				
Paraceras (10 spp.)†	(*hamatum*)			(*sauteri*)	(*melis*) (*crispis*)	1 n. sp.	(1 n. sp.)	(1 n. sp.)		(*javanicum*)		(*pendleburyi*)		
(Totals)	(1)			(1)	(2)	(1)	(1)	(1)		(1)		(1)		

Names in parentheses indicate species which infest carnivores or rats, not squirrels.
* = One new species of *Macrostylophora* occurs both on Borneo and Taiwan, on *Dremomys*.
† = Includes *P. melinum* whose host and type-locality are unknown but which Jordan (1939) believed was from 'tropical Asia'.

and a Neotropical one of 5 species, but there are no known Nearctic taxa. Thirty of the 32 (94%) remaining genera are limited to the Australian, Wallacean or Oriental Regions, and only 3 occur on the Asian mainland, where they are relatively poorly represented insofar as concerns species. There are 170 species known to me in these 30 genera, and 137 (80%) of these are restricted to the Australo-Asian Archipelagoes.

A break-down of the genera (and species-groups representing unnamed genera) occurring in the Oriental Region and Wallacea is shown in Table 4. (*Lentistivalius* is deleted therefrom but has been treated above.) As can be seen, 11 species (52%) of the known total of 21 *Medwayella* are found in Borneo, but 3 of these also occur elsewhere. *Medwayella* is relatively rich in species in Malaya, where 6 (29%) have been reported, but the maximum number elsewhere is 3 (Thailand and Java). The low numbers in the other Oriental areas are noteworthy, even though the totals for Sumatra and Java probably reflect inadequate collecting. Enough field-work has been done in Thailand, Indo-China and Mindanao to indicate that the total number of *Medwayella* therein must be substantially lower than in Malaya or Borneo. Further, Malaya has been well studied, but it seems likely that additional new species of *Medwayella* await discovery in Borneo, especially in Kalimantan and Sarawak. Additional data on the distribution of *Medwayella* are presented in Tables 5 and 7 where the hosts are treated.

All of the other genera are represented by but 1 or 2 species, with the exception of *Stivalius s. str.*, which consists of 5 species (all on the subgenus *Rattus*), of which 3 are Indian. It is noteworthy that the *S. jacobsoni* group and the *S. mjoebergi* group, both listed for 2 species, each includes a widespread species which occurs on the mainland, namely, *S. jacobsoni* (Jordan & Rothschild, 1922) and *S. klossi* (Jordan & Rothschild, 1922) respectively. The new species in Borneo is likewise found on Palawan. It is stressed that virtually no fleas are known from Celebes, and I am certain that a rich fauna of pygiopsyllids awaits discovery there.

2. Callosciurine Fleas

Because *Medwayella* is so intimately associated with Oriental squirrels, data on squirrel-fleas of that Region are presented in Tables 5 and 6. However, it should be borne in mind that squirrels are common in the Palaearctic and Nearctic Regions, and even in the Ethiopian Region as well, and that there they carry different kinds of fleas. Such data on northern and African squirrels are summarized later (p. 410 and Tables 8 and 9).

In Table 5 are listed the species of callosciurine fleas which occur in the Burmo-Chinese and Malayan Subregions, as well as other members of those genera which infest other hosts in the areas specified. In the latter category are fleas of rats and carnivores, and the names of these fleas are shown in parentheses. Of the remainder, which are sciurid-fleas, *Macrostylophora fimbriata* (Jordan & Rothschild, 1921) is a Himalayan flying-squirrel flea. (Other squirrel-fleas, besides those listed, occur in the Palaearctic areas cited, e.g. *Monopsyllus* Kolenati, 1857, but since such genera are not represented in these Oriental Subregions, they are deleted from the Table. Fleas of funambuline squirrels are likewise unlisted, since either they are absent

from the pertinent Subregions, e.g. *Funambulus* Lesson, 1835, or else are not yet known to have specific fleas, if any at all, i.e. *Ratufa* Gray, 1867.[2]) In the approximate geographic area being treated, there are two genera of squirrels for which we regrettably have no data, namely the monotypic *Rheithrosciurus*[2] in Borneo and *Prosciurillus* Ellerman, 1947[2] (3 species) in Celebes.

There are 21 species of *Medwayella* in Table 5, and 5 of these are found in more than one area. *M. robinsoni* (Rothschild, 1905) ranges from Thailand to Sarawak. *M. thurmani* Traub, 1972, is reported from Indo-China and Thailand. *M. phangi* Traub, 1972, occurs in Malaya and Sarawak. *M. calcarata* Traub, 1972, occurs in Malaya and Sarawak, while *M. dryadosa* Traub, 1972, heretofore known only from Malaya, has just been discovered in Java, subsequent to the description of the species in the first article in this series. Three of the Malayan species are found in Sarawak.

The ceratophyllid genus *Macrostylophora* Ewing, 1929, is a characteristic parasite of callosciurine squirrels throughout the Burmo-Chinese and Malayan Subregions, and in at least parts of the Indian Subregion, ranging to Ceylon. It extends into extremities of the Palaearctic Region into what is here termed the Eastern Palaearctic Subregion rather than Oriental Region (despite the position on the map), namely the mesic mountains of the Indian subcontinent and Formosa. A total of 10 species of *Macrostylophora* have been described from the Himalayan–North Burma–southern China area (which includes both Palaearctic and Indian elements) despite the fact that relatively little collecting of squirrel-fleas has been undertaken there. One of these northern species, namely *M. hastata* (Jordan & Rothschild, 1921) ranges as far east and south as Indo-China and Malaya. Although we have intensively collected squirrel-fleas in Malaya, only 2 species have been found there, and but 4 in Sabah. The finding of 5 species on Mindanao (all new) is worthy of note. A good example of a species of flea sharing the range of its host is provided by *M. liae* Wang, 1957, which is found on *Tamiops swinhoei* (Milne-Edwards, 1874) in both southern China and Formosa. *Macrostylophora* undoubtedly infests squirrels in Sarawak despite the dearth of reports, and it would not be surprising if it accompanied *Callosciurus prevosti* and *C. notatus* to Celebes.

The genus *Syngenopsyllus* Traub, 1950, includes *S. calceatus* (Rothschild, 1905) which ranges from Thailand to Sumatra and Java, and 2 new species, 1 from Malaya and 1 from Indo-China. There is a total of 10 species in the genus *Paraceras* Wagner, 1916, but only 1, an undescribed species from Indo-China, infests squirrels. The remainder parasitize carnivores such as badgers or civets, and rats, and 3 of these are Palaearctic.

Table 6 deals with the fleas of the callosciurine hosts for which we have reasonably good data on Siphonaptera, listing the species by name or by rather self-evident abbreviations. New species are given alphabetical designations to permit discussion.

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[2] Moore (1959) placed the genus *Ratufa* off by itself in a special tribe, the Ratufini. Simpson (1945) and Morris (1965) included it in Funambulini. Another change made by Moore was to remove *Prosciurillus* from the Sciurini and place it in the Callosciurini. Both Moore and Simpson, using different characters, concluded that *Rheithrosciurus* (which Moore in 1959 and 1961*a* spelled *Reithrosciurus*) belongs in the Sciurini, and this means that this rarely-collected Borneo squirrel is more than 3000 miles distant from its nearest relative. This remarkably disjunct distribution is of great interest in zoogeography.

Squi

1. *Callo*

2. *Callo*

3. *Callo*

4. *Callo*

5. *Callo*

6. *Callo*

7. *Sund*
S. lor

8. *Tam*

9. *Drem*

10. *Laris*

11. *Mene*

12. *Rhin*

+ = M

TABLE 6

Major fleas of tree-squirrels (Nos 1–5), scansorial squirrels (Nos 7–8) and ground-squirrels in certain areas of the Oriental Region

Squirrels	Indo-China	Thailand	Malaya	Java	Sumatra	Borneo: Sarawak	Borneo: Sabah	Philippines: Palawan	Philippines: Mindanao
1 *Callosciurus caniceps*			*Med. rob.* *Syn. cal.*						
	+	+	+						
2 *Callosciurus hippurus*			*Med. rob.*				*Med.* n. sp. A		
			+		+	+	+		
3. *Callosciurus notatus*			*Med. rob.* *Syn. cal.*	*Med. rob.* *Syn. cal.*	*Med. rob.*	*Med. rob.*	*Macro.* n. sp. A		
		+	+	+	+	+	+		
4 *Callosciurus nigrovittatus*		*Med. rob.*	*Med. rob.*	*Med. rob.* *Med. jav.*	*Med. ang.*				
							Macro. n. sp. B		
		+	+	+	+	+	+		
5 *Callosciurus prevosti*			*Med. rob.*				*Med.* n. sp. A		
			+		+	+	+		
6. *Callosciurus* (Others)						*Med. phangi*		*Med.* n. sp. B	*Med.* n. sp. C
		Macro. hast.						*Macro.* n. sp. C	4 *Macro.* n. spp. D–G
	+	+	+	+	+	+	+	+	+
7. *Sundasciurus tennis* or *S. lowi*			*Med. rob.* *Med. phangi* *Macro. levis*			*Med. loncha*	*Med. veruta* *Med.* n. sp. D		
		+	+		+	+	+		
8 *Tamiops macclellandi*	*Macro. hast.* *Macro. pil.* *Macro. prob.*	*Macro. hast.*	*Macro. hast.*						
	+	+	+						
9. *Dremomys* (species)	*Med.* n. sp. E *Macro.* n. sp. H		*Med.* n. sp. F *Macro. hast.*				*Lent. vom.* *Macro. born.* *Macro.* n. sp. I		
	+	+	+			+	+		
10. *Lariscus insignis*			*Med. rob.* *Med. calc.* *Med. dry.*	*Med. rob.* *Med. dry.* *Macro.* n. sp. J *Macro.* n. sp. K	*Med. ang.* (?)	*Med. calc.* *Med. bati.*			
			+	+	+	+			
11. *Menetes berdmorei*	*Med. thurm.* *Med.* n. sp. E	*Med. thurm.* *Macro. hast.*							
	+	+							
12. *Rhinosciurus laticaudatus*			*Med. rob.* *Med. dry.* *Med. limi*			*Med. calc.*			
			+		+	+	+		

\+ = Mammal present in area indicated.

The distribution of the hosts is indicated by a '+', and it is stressed that in many instances data on Siphonaptera are lacking for certain important regions, in cases where the squirrels are major hosts elsewhere. This is true, for example, for *Rhinosciurus* in Sumatra and Borneo, *Dremomys* in Sarawak, most hosts in Indonesia, and tree-squirrels in Sarawak.

As shown in Table 6, the various species of *Callosciurus* (all tree-squirrels) are major hosts of *M. robinsoni* in Malaya, and this probably will prove to be the case throughout the range of that flea. A new species of *Medwayella* appears to be prevalent on *Callosciurus* on Palawan and a second species fairly common on such squirrels on Mindanao. *S. calceatus* has also been collected from a variety of*Callosciurus* from Thailand to Java, but actually these represent only a few records,and it may even be that this species will prove to be a flying-squirrel flea, or a nest-flea of squirrels living in very tall trees (Traub, 1972b). *Macrostylophora hastata*, which at a minimum ranges from Nepal to Indo-China, is not very host-specific, infesting several species of *Callosciurus* and *Dremomys*, etc. In marked contrast, 2 new species from Sabah (Mt Kinabalu) are highly specific: over 95% of the long series of '*Macro. A*' were collected from *C. notatus* and 90% of '*Macro. B*' were from *C. nigrovittatus* Horsfield, 1824, even though the 2 species of infested squirrels not only came from the same areas, but often the same trees. Moreover, the exceptions (5% for species '*A*' and 10% for species '*B*') came from other genera of squirrels, such as *Dremomys* or *Glyphotes*.

The specificity of these *Macrostylophora* for *C. notatus* and *C. nigrovittatus* in Sabah seems especially significant in view of the fact that these squirrels are not known to be infested with any *Macrostylophora* in Malaya, and, indeed, are intimately associated there with a species of flea which is apparently absent from Sabah, namely *Medwayella robinsoni*. No other species of flea was represented in the extensive collections from Malayan *C. nigrovittatus*, and 99% of the fleas from *C. notatus* there were *M. robinsoni* (Traub, 1972a). The other species of *Medwayella* occurring in Malaya are primarily fleas of ground-squirrels, as mentioned in the first article in this series.

The ground-squirrel *Dremomys* occurs on the Asian mainland from Nepal to south China to Indo-China and Malaya (with a total of 3 or 4 species) and is found in Borneo (1 endemic species) and Formosa (1 endemic species) but it has not been reported in Indonesia. Under these circumstances, it is not surprising that the Bornean, Malayan and Indo-Chinese species of fleas known to infest these various *Dremomys* are all different. The fact that a new species of *Macrostylophora* from *Dremomys* on Mt Kinabalu apparently occurs as a subspecies in Formosa on another species of *Dremomys* is of interest.

The 3 species of *Medwayella* associated with *Rhinosciurus* in Malaya have not been found on this host elsewhere, but, unfortunately, there are few records of any fleas from this host in other countries, so these data cannot be properly evaluated. A greater number of species of *Medwayella* (7) appear to infest the ground-squirrel *Lariscus insignis* than any other host. Moreover, 3 of these have been found in other countries besides Malaya, as indicated.

In contrast to the apparent predilection of *Medwayella* for ground-squirrels, *Macrostylophora* is intimately associated with truly arboreal squirrels. Thus,

only 1 species, *M. levis* (Jordan & Rothschild, 1922) is common on a scansorial species. (As noted, only 1 infests flying-squirrels.)

It should be noted that although none of the fleas listed for Sarawak in Table 6 were recorded for Sabah, and vice versa, there are 2 species which occur in both areas, as mentioned below.

3. Fleas of Tupaiids, Rats and Insectivores

Table 7 deals with the fleas of certain tupaiids, rats and insectivores in the Burmo-Chinese and Malayan Subregions. The various species of *Tupaia* seem to be important hosts of *Medwayella* wherever they have been examined, but almost invariably those fleas seem to be more prevalent on callosciurines in the area than on *Tupaia*. Thus, in Malaya, no *M. calcarata* and only 2% of the *M. limi* Traub, 1972, and 10% of the *M. dryadosa* came from *Tupaia* (Traub, 1972a). The only instances to the contrary concern species known from only a few specimens, or in areas where data are lacking on *Callosciurus* (e.g. Sarawak). Similarly, throughout its range, *Stivalius klossi* is more abundant on *Rattus* than on *Tupaia*. However, on Mt Kinabalu, *Lentistivalius vomerus* Traub, 1972, and *S. mjoebergi* Jordan, 1926, were more plentiful on *Tupaia* than on other hosts. The former species was also taken on the tree-shrew *Dendrogale* fairly frequently.

The geographic records on *Tupaia* do not modify the picture shown by the callosciurines, except in two instances. *S. mjoebergi* was originally described from *Tupaia* on Mt Murud in northern Sarawak, but was later found by our teams and colleagues to be abundant on Mt Kinabalu and Mt Trus Madi in Sabah. It has not been reported farther south in Sarawak, but nevertheless must be listed as occurring in both areas. The only other indigenous species known to do so is *Medwayella veruta* Traub, 1972. First found near the base of Mt Kinabalu, the species was later collected by us in Kapit District, Sarawak (Traub, 1972a). This latter record (which apparently represents a distinct subspecies) is based upon 1 specimen from *Tupaia*, personally collected at about 100 ft elevation on an intensive collecting trip of several weeks' duration, during which time several hundred squirrels, rats and tree-shrews were carefully examined for fleas. This illustrates how scarce fleas can be in the humid tropical lowlands, at least at times, and emphasizes that the gaps in our knowledge of the zoogeography of fleas are not merely due to failure to examine mammals in certain areas.

The current Bornean records of fleas from rats and insectivores, like those from the squirrels and most of those from *Tupaia*, also suggest there may be some basic differences in the faunae of Sarawak and Sabah, since all of the species listed are for Sabah alone. Collections from the montane regions of Sarawak may modify this impression somewhat, for the endemic species of *Sigmactenus* Traub, 1950, occurring in New Guinea and the Philippines are widespread and abundant on the subgenus *Rattus* in the mountains, and it would be expected that this was true for the Borneo species as well.

The data in Table 4 are also relevant regarding the distribution of rat-pygiopsyllids since 6 of the 9 taxa are essentially rat-fleas and, in addition, 1 species of the *Stivalius mjoebergi*-group, namely *S. klossi*, infests these murines. The rat forms

Hc
1. *Tupaia* (s]
2. *Dendrogal* (Tree-shre
3. *Rattus* (*Le* *alticola*-gr(
4. *Rattus* (*Le* *R. surifer*
5. *Rattus* (*Le*
6. *Rattus* (*M*
7. *Rattus* (*Ra*
8. *Rattus* (*Ra*
9. *Rattus* (*St*
10. *Rattus* (*St*
11. *Rattus* (sp(
12. *Hylomys s*
13. *Crocidura*
+ = Mamma

Table 7

Major fleas of tree-shrews (tupaiids) (Nos 1–2), rats (Nos 3–10) and insectivores in certain areas of the Oriental Region

Hosts	Indo-China	Thailand	Malaya	Java	Sumatra	Borneo: Sarawak	Borneo: Sabah	Philippines: Palawan	Philippines: Mindanao
1. *Tupaia* (species) (Tree-shrews)	*Med. thurm.* *Med.* n. sp. E *Stiv. klossi* +	*Med. thurm.* *Stiv. klossi* +	*Med. rob.* *Med. phangi* *Med. dry.* *Stiv. klossi* +	*Med. jav.* (?) +	*Med. arc.* (?) +	*Med. phangi* *Med. ver.* *Stiv. mjoe.* +	*Med. ver.* *Med.* n. sp. D *Lent. vom.* *Stiv. mjoe.* *Macro. born.* +	*Med.* n. sp. B +	
2. *Dendrogale melanura* (Tree-shrew)						+	*Lent. vom.* +		
3. *Rattus* (*Lenothrix*) *alticola*-group							*Sig. alt.* *Gryph. hop.* +		
4. *Rattus* (*Lenothrix*) *rajah* or *R. surifer*		*Stiv. klossi* +	*Stiv. klossi* *Roths. smiti* +	+ +	+ +	+ +	*Sig. alt.* +	+ +	
5. *Rattus* (*Lenothrix*) *whiteheadi*		+ +	+ +		+ +	+ +	*Gryph. hop.* +		
6. *Rattus* (*Maxomys*) *fulvescens*			*Stiv. jacob.* +	*Stiv. jacob.* *Roths. kop.* +	+ +	+ +	*Stiv.* n. sp. A +		
7. *Rattus* (*Rattus*) *baluensis*							*Pyg. tip.* +		
8. *Rattus* (*Rattus*) (species)	*Stiv.* (*S*) *apor.* *X. vex.* +	*Stiv.* (*S*) *apor.* *X. vex.* *Parac.* n. sp. A +	+ +	*Stiv.* (*S*) *cog.* *Stiv. jacob.* *Neo. sond.* +	+ +	+ +	+ +	+ +	*Stiv.* (*S*) *cog.* *Stiv. pom.* *X. vex.* *Sig. wer.* +
9. *Rattus* (*Stenomys*) *bowersi*	*Neo. dispar* *Neo. avida* *Neo. tric.* +	*Neo. dispar* +	*Neo. dispar* *Parac.* n. sp. B +						
10. *Rattus* (*Stenomys*) *infraluteus*							*Neo. luma* +		
11. *Rattus* (species)	*Stiv. klossi* +	*Stiv. klossi* +	*Stiv. klossi* *Stiv. jacob.* *Parac* n. sp. B +	*Stiv. klossi* *Stiv. jacob.* *Neo.* n. sp. *Roths. kop.* +	*Stiv. klossi* *Stiv. jacob.* +	+ +	*Stiv.* n. sp. A *Sig. alt.* +	*Stiv.* n. sp. A +	*Sig. wer.* +
12. *Hylomys suillus* (Gymnure)	+	+	+	*Crat. bart.* +	+	+	*Crat. audyi* *Crat. crypt.* +		
13. *Crocidura* (Shrews)	+	+	*Pal. apsid.* +	*Pal. laxata* +	+	+	+	+	+

+ = Mammal present in area indicated.

are *Stivalius* (*s. str.*); *Gryphopsylla* Traub, 1957;[3] the *S. jacobsoni*-group; the *S. pomerantzi*-group; the new genus from the Philippines and *Pygiopsylla* (on Borneo, at least).

Many of the species listed for rats in Table 7 (and alluded to in Table 4) have a fairly broad range and are relatively non-specific, e.g. *S. klossi*, which is found on various subgenera and species of forest-rats from Indo-China to Sumatra, and *S. jacobsoni*, which is known from Malaya, Sumatra and Borneo and infests similar hosts. The dearth of records of *S. klossi* from members of the subgenus *Rattus* is notable, even though occasional specimens are found on the wild forms. The new species on a variety of rats on Mt Kinabalu exists as a subspecies on Palawan and apparently is a derivative of *S. jacobsoni*. The rat with the maximum range is *R.* (*Maxomys*) *fulvescens* (Indo-China to Sabah), but no records of its fleas exist for much of the territory. The new genus listed in Table 4 is from Mindanao and presumably is a parasite of an endemic genus of rat and is related to the pygiopsyllids associated with New Guinea and the *S. celebensis*-group of New Guinea.

Rats of the subgenus *Rattus* are found throughout the Oriental, Wallacean and Australian Regions, and many indigenous species are represented, as well as commensal ones. As expected, their fleas include endemic, restricted and wide-spread species. *Stivalius* (*S.*) *aporus* Jordan & Rothschild, 1922, apparently as subspecies of an Indian form, exists in southern China, Indo-China and Thailand (Traub, 1972a). *S.* (*S.*) *cognatus* Jordan & Rothschild, 1922, is known from Java and the Philippines (Mindanao and Luzon), again as subspecies, and probably occurs elsewhere in the Subregion. *Stivalius pomerantzi* Traub, 1951, apparently represents a distinct genus and has been found on several of the islands of the Philippines (Mindanao, Negros and Leyte). *Pygiopsylla tiptoni* Traub, 1957, a characteristic flea of *R. baluensis* (Thomas, 1894), is indigenous to Mt Kinabalu, and its nearest known relatives are in New Guinea and Australia. (It appears significant that Misoune (1969) presumably regarded this rat as belonging in the subgenus *Bullimus* Mearns, 1905, near *R. xanthurus* (Gray, 1867) of Celebes, and not in the subgenus *Rattus*. Sody (1941) and others treated it as a subspecies of *R. rattus* (Linnaeus, 1758). Ellerman (1941) and Medway (1963) viewed it as a full species in the subgenus *Rattus*, and Medway (p. 122) emphasized it 'is very distinct . . . separated . . . by both morphology and habit'.)

Several non-pygiopsyllids are associated with the subgenus *Rattus*. The one with the broadest range is *Xenopsylla vexabilis* Jordan, 1925 (Pulicidae) which has been collected in Australia, New Guinea, Mindanao, Java, Indo-China and Thailand. The main host on the mainland is *Rattus berdmorei* (Blythe, 1851) (which is in the subgenus *Bullimus* according to Misoune (1969) but in the subgenus *Berylmys* Ellerman, 1947, fide Ellerman & Morrison-Scott (1951)). However, it is also found on the subgenus *Rattus* on Continental Asia, and primarily so, usually on commensal forms, on the Pacific Islands. *X. vexabilis* has also been introduced into Hawaii via commensal rats. It should be noted that there are other *Xenopsylla* Glinkiewicz, 1907, in the Burmo-Chinese Subregion and the Australian Region

[3] NEW STATUS. This was heretofore treated as a subgenus of *Stivalius*.

which are endemic (and specialized) and which are not associated with the subgenus *Rattus*, namely *X. papuensis* (Jordan, 1933) on certain species of the phloeomyine murid genus *Pogonomys* Milne-Edwards, 1877, in New Guinea and a new species on an indigenous rat in the mountains of Luzon.

4. *Leptopsylla* and Allies

Of special interest is the occurrence of members of the family Leptopsyllidae in the Burmo-Chinese and Malayan Subregions, 2 of which, *Sigmactenus werneri* Traub, 1950, and *S. alticola* Traub, 1954, are listed in Table 7. The genus *Sigmactenus* is akin to *Leptopsylla* Jordan & Rothschild, 1911, along with *Peromyscopsylla* I. Fox, 1939, and the 3 genera include a total of 36 species. Of this total, 26 are Palaearctic, 3 Oriental, 1 Australian, 1 Ethiopian, 6 Nearctic, and 2 are Holarctic (Traub, in prep.). There are 3 species of *Sigmactenus* and all infest rats: *S. werneri*, on Mindanao and Negros in the Philippines; *S. alticola*, on Mt Kinabalu, etc., in Sabah, and *S. toxopeusi* Smit, 1953, in New Guinea. The existing records of *S. alticola* are from forest-rats, primarily *R.* (*Lenothrix*) *alticola* in a habitat where there were no rats of the subgenus *Rattus*. At least one of the others (*S. werneri*) is common on (*Rattus*), and this may prove to be the case for *S. alticola* in other parts of Borneo.

Sigmactenus is most closely allied to *Leptopsylla* (*Pectinoctenus*) Wagner, 1928, a Palaearctic taxon, which includes 6 species, 5 of which infest the murine *Apodemus* Kaup, 1829, and 1 of which parasitizes cricetids. The subgenus *Leptopsylla* includes 9 species of which 8 are Palaearctic (5 on murines) and 1 Ethiopian (on rats). Only 1 of the 18 species of *Peromyscopsylla* infest murines; 12 occur on microtines and 7 of these are Nearctic and 2 Holarctic; the remaining 8, Palaearctic. There are 4 Nearctic *Peromyscopsylla* ex *Peromyscus* Gloger, 1841, and 1 Palaearctic species associated with *Calomyscus* Thomas, 1905, a cricetine.

Except for the 2 species of *Sigmactenus*, the only leptopsyllid allied to *Leptopsylla* which is known from the Oriental Region is a species of *Peromyscopsylla* which is either *P. himalaica* (Rothschild, 1915) or a sibling derivative thereof, resident on *Rattus* in the mountains of central Luzon. *P. himalaica* is a far-ranging species known from Taiwan, Japan, and northern India, where it infests *Rattus* or *Apodemus*. (This is apparently the first faunal record in the Philippines of a non-commensal species with Palaearctic affinities, and it is noteworthy that along with this *Peromyscopsylla*, there was taken another leptopsyllid, *Frontopsylla nakagawai* Kumada & Sakaguti, 1959, an amphipsylline, previously known from Japan and Taiwan, where it infests *Apodemus*.)

5. *Neopsylla* and Allies

Another taxon in Table 7 which is of definite northern (Palaearctic) affinity is the hystrichopsyllid genus *Neopsylla* Wagner, 1903 (Neopsyllinae). The 11 genera of this subfamily are all allied and encompass a total of 88 species for which I have data. Nine of the genera, including 57 of the species, are found in either the Nearctic or Palaearctic Regions (or both) and nowhere else. Only 2 genera, *Neopsylla* and *Rothschildiana* Smit, 1952, occur in the Oriental Region, and these merit further

consideration. There are 29 species of *Neopsylla*, for which we have reliable host-data, and of these, 1 is Nearctic, 20 are Palaearctic and 9 are Oriental (of which 1 also occurs in the Palaearctic Region). Eight of the 9 Oriental species are parasites of rats; the exception is the south Chinese species which also is Palaearctic. Fifteen of the 29 *Neopsylla* under discussion are rat-fleas; the remainder infest sciurids and cricetines. The genus *Neopsylla* was divided into two groups, the *N. stevensi*-group and the *N. setosa*-group, purely on the grounds of leg-chaetotaxy by Hopkins & Rothschild (1962), but, interestingly enough, the classification extends to the hosts as well, for the *N. stevensi*-group includes all the *Rattus*-fleas. Seven of these rat-*Neopsylla* are Palaearctic and 8 are Oriental. Five rat-*Neopsylla* are listed in Table 7: 3 from Indo-China, of which *N. dispar* Jordan, 1932, extends into Malaya; *N. sondaica* Jordan, 1931, on Java and *N. luma* Traub, 1954, in Sabah. (The remaining 3 are from southern China.) The 3 Indo-Chinese species infest *R.* (*Stenomys*) *bowersi*, as does *N. dispar*. *N. luma* is closely related to *N. dispar*, and it is of interest that its host, *R.* (*S.*) *infraluteus*, is allied to *R.* (*S.*) *bowersi*. The true hosts of *N. sondaica* are unknown.

The second Oriental neopsylline genus, *Rothschildiana*, is essentially a somewhat specialized *Neopsylla* and is known from 2 species: 1 Malayan, associated with the *R.* (*Lenothrix*) *rajah*-group, and the other, with *R.* (*Maxomys*) *fulvescens* on Java. All together, a total of 11 species of Neopsyllines occur in the Oriental Region, 4 of these in the Malayan Subregion.

6. Ceratophyllid Rat-Fleas

In general, there are relatively few ceratophyllid fleas infesting rats. One exception is the genus *Nosopsyllus* Jordan, 1933, which, while present in India, is not known to extend into the Malayan or Burmo-Chinese Regions. (It may be present in Burma, etc.) *Paraceras* is another, and as noted, 7 or 8 of the 10 species are Oriental, but at least 1 of the Palaearctic species is European. There are 2 *Paraceras* listed in Table 7, both new to Science. One is from an unidentified species of the subgenus *Rattus* in Thailand, and the second a common parasite of *R.* (*M.*) *fulvescens* in the mountains of Malaya.

7. Insectivore-Fleas

Relatively little is known about insectivore-fleas in the Oriental Region in general and especially in the Southeastern and Malayan Subregions. Two genera have been reported for the Malayan Subregion, however, viz., the leptopsylline *Cratynius* Jordan, 1933, and the hystrichopsyllid *Palaeopsylla* Wagner, 1903. *Cratynius* is presumably a fairly specific flea of the lesser gymnure *Hylomys suillus*, a monotypic erinaceid that ranges from Indo-China to Borneo, but the only records of the fleas are from Java (1 species) and Sabah (2 species). Except for *Palaeopsylla*, there are no Ctenophthalminae in the Oriental Region, and 23 of the 27 contemporary *Palaeopsylla* occur in the Palaearctic Region. There are but 5 known from the Oriental Region, and 1 of these is Palaearctic as well. Three of the Oriental ones are from south China. The Malayan and Javanese species (Table 7) were both collected on shrews in the mountains.

8. Squirrel-Fleas in General

As a basis for discussing the possible origins and affinities of *Medwayella*, it is advisable to consider the distribution and background of all genera of fleas which include species infesting tree-squirrels (including flying-squirrels). Such data are summarized in Tables 8 and 9, but it should be noted that the fleas of spermophiles, chipmunks and marmots are deleted therefrom because such hosts, by virtue of their nesting underground, and their intimate contact with the habitat of other ground-level rodents, have acquired fleas that are characteristic of, or akin to, those of such neighbouring mammals. *Xerus* Ehrenberg, 1833, and other African ground-squirrels are not represented because their flea fauna is insufficiently known and they too have acquired some atypical fleas.

As can be seen from Table 8, there is a rich fauna of fleas associated with tree-squirrels and semi-arboreal squirrels, e.g. 22 genera, representing 3 families and encompassing 109 species (out of the total of 293 belonging to those genera). It should be borne in mind, however, that the distribution indicated pertains to the genus as a whole, and not merely to the component infesting squirrels. Thus, in the case of the pygiopsyllid *Lentistivalius*, the single species on squirrels is found in Borneo, but the genus includes African and Japanese species on other hosts. Similarly, the genus *Monopsyllus* is Holarctic in the sense that representatives are found in the Nearctic and Palaearctic Regions, but only 1 of the species is truly Holarctic (namely *M. tolli* (Wagner, 1901) on *Ochotona* Link, 1795). The only Holarctic squirrel-flea is *Tarsopsylla octodecimdentata* (Kolenati, 1863).

Only 3 of the 16 recognized families of Siphonaptera have fleas characteristically infesting arboreal or semi-arboreal squirrels, namely the Hystrichopsyllidae, Pygiopsyllidae and Ceratophyllidae. There are 45 genera of Hystrichopsyllidae, and 33 (74%) of these are found in the 'holarctic' regions, with 12 (27%) in the border or transitional parts of those Regions, but with only 4 (9%) occurring in the Oriental Region (Traub, in prep.). (Some of these genera are found in more than one area, e.g. 2 of the Oriental hystrichopsyllid genera are also found in the Palaearctic, and 1 of those is Holarctic.) The Ceratophyllidae is essentially a northern family, i.e. 28 of 31 (90%) genera infesting non-volant hosts are found in the northern Regions, while only 5 (16%) are Oriental, and 3 of those are Palaearctic as well. (Additional generalizations about the northern affinities of ceratophyllids are presented in the Discussion (p. 423). As has been shown, the pygiopsyllids are very poorly represented in the north, with only 1 species of 1 genus being Palaearctic and none Nearctic.

The association with squirrels is relatively rare in the Hystrichopsyllidae (in only 4 of 45 genera—none Oriental) and Pygiopsyllidae (2 of 33 genera). In contrast, squirrel-fleas are known in 16 genera of Ceratophyllidae, and of the total of 196 species of fleas in such genera, 81 actually infest squirrels. It also seems significant that the hystrichopsyllid genera associated with squirrels are presumably nest-fleas, and that in each case only 1–2 of the species are involved (e.g. 2 of 52 *Rhadinopsylla* Jordan & Rothschild, 1912), the remainder being associated with other hosts. Similarly, among pygiopsyllids, 4 of the 5 known *Lentistivalius* para-

TABLE 8

Genera of Siphonaptera with species infesting arboreal or scansorial squirrels

Squirrel-fleas Genera and their distribution		Numbers of fleas and their major hosts: Total in genus or genera	On squirrels*	On other hosts
Hystrichopsyllidae	4 genera	71	6	65
Conorhinopsylla	(Nests) Nearctic	2	1	1 (*Neotoma*)
Epitedia	(Nests) Nearctic	8	1	7 (*Neotoma, Peromyscus*)
Megarthroglossus	(Nests) Nearctic	9	2	7 (*Neotoma*)
Rhadinopsylla	(Nests?) Holarctic	52	2	50 (Microtines, Cricetines)
Pygiopsyllidae	2 genera	26	22	4
Lentistivalius	Ethiopian, Oriental and Palaearctic	5	1	4 (Birds, Shrews, Murines, *Tupaia*)
Medwayella	Oriental	21	21	1 (?) (*Tupaia*?)
Ceratophyllidae	16 genera	196	±81	±112
Aenigmopsylla	Palaearctic	1	1	0
Brevictenidia	Palaearctic	1	1	0
Hollandipsylla	(Borneo)	1	1	0
Kohlsia	Temp. Mid. Amer. and Transitional	21	1	20 (Peromyscini)
Libyastus	Ethiopian	15	14	1 (Dormouse)
Macrostylophora	Oriental and Palaearctic	28	28	0
Monopsyllus	Holarctic	22	6	14 (Chipmunks, Cricetines)
Nosopsyllus	Palaearctic, Oriental and introduced	46	6	40 (Gerbillines, Murines, etc.)
Opisodasys	Nearctic	9	7	2 (*Peromyscus*)
Orchopeas	Nearctic, including Temp. Mid. Amer.	13	7	6 (*Peromyscus, Neotoma*)
Paraceras	Palaearctic and Oriental	9	1	8 (Carnivores, Rats)
Pleochaetis	Temp. mid. Amer. and Transitional	23	1 (2?)	22 (21?) (Peromyscini)
Syngenopsyllus	Oriental	3	3	0
Tarsopsylla	Holarctic	1	1	0
New genus No. 1	Palaearctic	1	1	0
New genus No. 2	Palaearctic	1	1	0

* = Excludes chipmunks, spermophiles, marmots, *Xerus* ground-squirrels, etc. (flying-squirrels *are* included).

sitize non-sciurids, but all of the 21 species of *Medwayella* infest squirrels. In the ceratophyllids, there is unanimity in the large genus *Macrostylophora* in this regard, while 14 of 15 *Libyastus* Jordan, 1936, and 7 of 9 *Opisodasys* Jordan, 1933, have squirrels for hosts. As Jellison has pointed out (1945), 4 genera of North American Siphonaptera, namely *Conorhinopsylla* Stewart, 1927, *Monopsyllus*, *Opisodasys*

and *Orchopeas* Jordan, 1933, have 1 or more species occurring on tree-squirrels, and 1 or more on *Peromyscus* or *Neotoma* Say & Ord, 1825 (Cricetinae, Peromyscini). We now realize the *Epitedia* Jordan, 1938, *Megarthroglossus* Jordan & Rothschild, 1915, *Pleochaetis* Jordan, 1933, and *Kohlsia* Traub, 1950, are also in this category, as is *Rhadinopsylla*. The phenomenon of joint infestation of sciurid and peromyscine hosts by a single genus thus occurs in both Ceratophyllidae and Hystrichopsyllidae.

In some instances only a minority of the ceratophyllid species are involved in the relationship with squirrels, viz., 1 or 2 of 23 *Pleochaetis*, 1 of 21 *Kohlsia*. It is of interest that the squirrel-infesting *Nosopsyllus* are all in the Indian Subregion (where they infest *Funambulus*, a lowland group of 'palm-squirrels'), whereas the bulk of the 46 species are on murines or, in xeric areas, on gerbillines.

It should be noted that some of the ceratophyllid genera are known only from fleas associated with flying-squirrels, namely *Hollandipsylla* Traub, 1953, on *Hylopetes* Thomas, 1908, and the 2 new genera listed as No. 1 and No. 2, which are from Pakistan, on *Hylopetes* and *Petaurista* Link, 1795, respectively, in an area where ordinary tree-squirrels are unknown. In certain instances, a few of the species of a genus infest flying-squirrels while the bulk of them parasitize tree-squirrels, e.g. 2 of the 7 squirrel-*Opisodasys* (*O. pseudarctomys* (Baker, 1904) and *O. vesperalis* (Jordan, 1929)); 1 of the 28 *Macrostylophora* (*M. fimbriata*); 1 of the 7 *Orchopeas* of squirrels, namely, *O. bolivari* Barrera, 1955 (new status)[4]; and 1 of the pertinent 6 *Monopsyllus* (*M. argus* (Rothschild, 1908)). The Holarctic monotypic *Tarsopsylla* Wagner, 1927, may turn out to be a flea of flying-squirrels. (While the majority of records of the hystrichopsyllid *Rhadinopsylla japonica* Sakaguti & Jameson, 1956, are from flying-squirrels, I believe that this species is really a flea of the nests of such hosts.)

True nest-fleas appear to be rare among the species of Ceratophyllidae infesting sciurids. *Hollandipsylla* may be one. The status of *Syngenopsyllus*, *Libyastus*, *Tarsopsylla* and the 2 *Opisodasys* parasitizing flying-squirrels have been discussed in the second article in this series and their special modifications may be adaptive and correlated with the habits of the hosts.

The zoogeographic distribution of the genera which possess species infesting arboreal and semi-arboreal squirrels is summarized in Table 9. Here the picture is complicated by the fact that a wide-ranging genus may be associated with squirrels on only a limited part of its range, and only a few of its species may be involved in this manner, e.g. *Nosopsyllus* on the Indian subcontinent. As a result, it is necessary to consider the distribution of *all* the species in those genera in which some members parasitize squirrels, and to consider the precise regions in which this phenomenon occurs. This information is also summarized in the table. Further, since some of the Nearctic genera richest in species are restricted to the mountains of Mexico and Middle America (and the northern tip of South America), this Temperate Middle American Subregion has been treated separately from the rest of the Nearctic Region.

The Australian Region is omitted from Table 9 not only because squirrels do not occur there, but because genera of fleas associated with these hosts elsewhere are likewise absent. *Medwayella* is the nearest known representative and it is found no

[4] In the original description this species was referred to as *O. howardi bolivari*.

TABLE 9

Distribution of fleas of arboreal and semi-arboreal squirrels, i.e. excluding fleas of chipmunks, spermophiles, etc., with total numbers of genera and species per constituent families. (Fleas of volant hosts deleted)

	Family totals	Nearctic Temp. Mid. Amer.	Nearctic (Other)	Palae-arctic	Oriental	Ethio-pian	Intro-duced†
Hystrichopsyllidae							
Total number genera in area	45	10^{6H-2*}	25^{10H-2*}	18^{10H}	4^{H-2*}	3^{H}	
Total number species in area for those genera (all hosts)	443	34*	110*	19^{1H}	63	69	
Number of local genera infesting squirrels anywhere	4	1^{H}	4^{H}	1^{H}			
Total number species in such squirrel-genera (all hosts, all areas)	68	49	71	49			
Number of squirrel-species in all areas	6	2	6	2			
Number of species on squirrels in specific areas	6		5	1			
Pygiopsyllidae							
Total number genera in area	33			1*	10	2	
Total number species in area for those genera (all hosts)	177			2*	35*	14	
Number of local genera infesting squirrels anywhere	2			1*	2*	1*	
Total number species in such squirrel-genera (all hosts, all areas)	26			5	26	5	
Number of squirrel-species in all areas	22			1	22	1	
Number of species on squirrels in specific areas	22				22		
Ceratophyllidae							
Total number genera in area	31	11^{3H-10*}	16^{8H-10*}	19^{8H-3*}	5^{3*}	2*	2
Total number species in area for those genera (all hosts)	312	77^{14*}	82^{6H-14*}	105^{6H-*}	47*	16	3
Number of local genera infesting squirrels anywhere	16	5^{H}	5^{2H}	9^{2H-2*}	5^{3*}	2*	2
Total number species in such squirrel-genera (all hosts, all areas)	196	86?*	66^{H-7*}	111^{2H-*}	88	61	66
Number of squirrel-species in all areas	81	22^{2*}	22^{H-2*}	47^{H}	40	21	12
Number of species on squirrels in specific areas	81	8^{2*}	13^{2*}	18^{H}	38	15	

H = Holarctic genus or species.
* = One genus or species occurs in more than one area.
† = Genera like *Monopsyllus* and *Nosopsyllus*, which include some introduced species.

closer than Indonesia and the Philippines. The Neotropical Region is also not included, for no squirrel-fleas have been found there even though a few squirrels are endemic, as extensions of the Nearctic fauna in the northern mountains.[5]

From Table 9 it can be seen that only 6 of 443 species of hystrichopsyllid fleas are associated with arboreal or semi-arboreal squirrels and only 22 of 177 pygiopsyllid fleas infest such hosts. In contrast, 81 of 316 species of ceratophyllid fleas of non-volant hosts are found on these sciurids. Of the 6 hystrichopsyllid species, 5 are Nearctic and the sixth Palaearctic (Japan), while all of the 22 pygiopsyllids on squirrels are Oriental (and, as we have seen, 21 of these are in *Medwayella*).

Ceratophyllid squirrel-fleas are found in all four Regions listed, and insofar as concerns numbers of species, are better represented in the Oriental Region than in the others, and nearly as well in the Ethiopian Region as in the Nearctic and Palaearctic. However, there are significant differences in other respects, due to the fact that very few ceratophyllid genera are present in the Oriental and Ethiopian Regions, and those that do occur, infest squirrels there and elsewhere. In contrast, in the Palaearctic and Nearctic Regions, squirrel-ceratophyllid genera are not only in the minority, but generally include many species which parasitize other hosts. These points are shown by the following figures. Five of the 11 genera of ceratophyllids occurring within the Temperate Middle American Subregion infest squirrels somewhere in their range. (Four of these, namely *Kohlsia*, *Pleochaetis*, *Opisodasys* and *Orchopeas*, parasitize such hosts within the Subregion; the fifth, *Monopsyllus*, is known from chipmunks in Mexico, but species infesting tree-squirrels occur in other Nearctic subregions and in the Palaearctic.) These 5 genera include a total of 86 species, of which 22 are associated with squirrels, with 8 such species occurring within the Subregion. There are 69 ceratophyllid species in the area (90% of the total) which do not infest the sciurids under discussion. In the remainder of the Nearctic Region, there are also 5 ceratophyllid genera which include squirrel-fleas (of a total of 16), namely 4 of the 5 more southern ones, but with *Tarsopsylla* replacing *Kohlsia*, which does not occur north of the Temperate Middle American Subregion. (Moreover, the 1 or 2 squirrel-species of *Pleochaetis* are unknown north of southern Mexico.) A total of 66 species are found in these 5 genera, and 22 of these are squirrel-fleas, of which 13 occur in the Subregions in question, the residue being Temperate Middle American or Palaearctic. A total of 69 (84%) of the ceratophyllids in the Region infest other kinds of hosts. A similar picture is presented by the Palaearctic fauna. Thus, 9 of 19 genera are associated with arboreal or semi-arboreal squirrels, and these genera include 105 species, of which 47 infest squirrels somewhere within the range of the genera. However, it is important to note that these figures include *Macrostylophora*, of which only 2 of the 28 species are Palaearctic, the remainder being Oriental. There are 18 species of squirrel-fleas in the

[5] Squirrel-fleas very likely occur in the mountainous part of South America, but have not yet been reported, although little collecting has been done there. *Pleochaetis dolens quitanus* (Jordan, 1931) has been described from *Oryzomys* Baird, 1857, and *Thomasomys* Coues, 1884, in Ecuador, while the nominate form, from Central America, is common on squirrels. It is believed that sciurids occur in that part of Ecuador. Moreover, some *Thomasomys* are arboreal, and the *P. dolens quitanus* may hence be strays from squirrels. Sciurids are found in South America as far south as northern Argentina.

Palaearctic Region, but 87 ceratophyllids which do not infest squirrels likewise occur there, and these total 83% of the species known.

The situation is quite different in the more southern Regions. In the Oriental Region, all 5 of the endemic ceratophyllids have species infesting squirrels. (As will be stressed later in another article, no ground-dwelling cricetids, which are the major hosts of ceratophyllids, occur there.) Of the 49 species of Oriental ceratophyllids, 37 are squirrel-fleas. The exceptions are largely members of *Nosopsyllus* on gerbillines and murids (which are the main hosts of the genus, there being only 6 squirrel-species, all on *Funambulus* on the Indian subcontinent). Of the 10 species of *Paraceras* known to me, only 1, an undescribed species from Indo-China, infests sciurids; the remainder parasitize carnivores or murids. However, the Formosan *P. sauteri* (Rothschild, 1914), when better known, may turn out to be a squirrel-flea, since most of the records are from arboreal carnivores.

Similarly, in the Ethiopian Region (where there also is a dearth or literal absence of ground-dwelling cricetids), ceratophyllids are relatively scarce. There are only

TABLE 10

Distribution of certain mammals in Malaya, Sumatra, Java and Borneo

Species	Malaya	Sumatra	Java	Borneo
Tupaia glis	+	+	+	+
Tupaia minor	+	+		+
Tupaia tana	+	+		+
Ptilocercus lowi	+	+		+
Callosciurus hippurus	+	+		+
Callosciurus nigrovittatus	+	+	+	+
Callosciurus notatus	+	+	+	+
Callosciurus prevosti	+	+		+
Dremomys (species)	+			+
Lariscus insignis	+	+	+	+
Rhinosciurus laticaudatus	+	+		+
Sundasciurus lowi or *S. tenuis*	+	+		+
Pithecheir melanurus	+	+	+	
Rattus (*Lenothrix*) *canus*	+	+		+
Rattus (*Lenothrix*) *rajah* or *R. surifer*	+	+	+	+
Rattus (*Lenothrix*) *whiteheadi*	+	+		+
Rattus (*Leopoldamys*) *sabanus*	+	+	+	+
Rattus (*Maxomys*) *fulvescens*	+	+	+	+
Rattus (*Stenomys*) *muelleri*	+	+		+
Echinosorex gymnurus	+	+		+
Hylomys suillus	+	+	+	+

2 such genera with a total of 16 species. Of these, 15 occur in the endemic African genus *Libyastus*, with 14 species on tree-squirrels. The remaining endemic ceratophyllid is a murine-species of *Nosopsyllus* (which genus is well represented in the Palaearctic Region of Africa on murines and gerbillines).

Certain wide-ranging and introduced forms, such as *Nosopsyllus fasciatus* (Bosc., 1801), *N. londiniensis* (Rothschild, 1903), *Monopsyllus anisus* (Rothschild, 1907), etc., have been treated in a special column in Table 9. The first-named is of probable Indian origin; the remainder Palaearctic.

Table 11

Species of fleas of non-volant hosts* known from Malaya, Java, Sarawak and Sabah. (Wide-ranging fleas of commensals excluded)

Malaya	Java	Sarawak	Sabah
Medwayella robinsoni	*Medwayella robinsoni*	*Medwayella robinsoni*	
Medwayella phangi		*Medwayella phangi*	
Medwayella calcarata		*Medwayella calcarata*	
Medwayella dryadosa	*Medwayella dryadosa*		
		Medwayella veruta	*Medwayella veruta*
Medwayella limi	*Medwayella javanica*	*Medwayella batibacula*	*Medwayella* n. sp. *'A'*
Medwayella n. sp. *'F'*		*Medwayella loncha*	*Medwayella* n. sp. *'D'*
		Medwayella rhaeba	*Medwayella* n. sp. *'G'*
			Medwayella n. sp. *'H'*
			Gryphopsylla hopkinsi
*Lentistivalius insolli**			*Lentistivalius vomerus*
			Pygiopsylla tiptoni
Stivalius jacobsoni	*Stivalius jacobsoni*		*Stivalius* n. sp. *'A'*
Stivalius klossi	*Stivalius klossi*		
		Stivalius mjoebergi	*Stivalius mjoebergi*
	Stivalius (s. s.) *cognatus*		
Macrostylophora hastata	*Macrostylophora* n. sp. *'J'*		*Macrostylophora borneensis*
			Macrostylophora n. sp. *'A'*
Macrostylophora levis	*Macrostylophora* n. sp. *'K'*		*Macrostylophora* n. sp. *'B'*
			Macrostylophora n. sp. *'I'*
Paraceras n. sp. *'A'*	*Paraceras javanicum*		*Paraceras pendleburyi*
Syngenopsyllus calceatus	*Syngenopsyllus calceatus*		
Syngenopsyllus n. sp. *'A'*			
Neopsylla dispar	*Neopsylla sondaica*		*Neopsylla luma*
	Neopsylla n. sp. *'A'*		
Palaeopsylla apsidata	*Palaeopsylla laxata*		
Rothschildiana smiti	*Rothschildiana kopsteini*		
	Cratynius bartelsi		*Cratynius audyi*
			Cratynius crypticus
Totals: 10 Genera	11 Genera	2 Genera	10 Genera
17 Species	15 Species	8 Species	18 Species

* = *Lentistivalius insolli* is a bird-flea, but other members of the genus infest mammals.

TABLE 12

Numbers of genera of fleas shared by Malaya, Java or Borneo (Sabah and Sarawak only), with names and zoogeographic (regional) affinities of absentees. (Fleas of non-volant hosts.*) (Wide-ranging fleas of commensals excluded)

Area and numbers of genera	Malaya			Java			Borneo (Sabah and Sarawak)		
	Numbers shared	Unknown in Malaya	Affinities of absentees	Numbers shared	Unknown in Java	Affinities of absentees	Numbers shared	Unknown in Borneo	Affinities of absentees
Malaya (10)	–	—	—	9	*Lentistivalius**	Australian	7*	*Syngenopsyllus* *Palaeopsylla* *Rothschildiana*	All Palaearctic
Java (11)	9	*Stivalius* (s. str.) *Cratynius*	Australian Palaearctic	–	—	—	7	*Stivalius* (s. str.) *Syngenopsyllus* *Palaeopsylla* *Rothschildiana*	Australian 3 = Palaearctic
Borneo (10)	7	*Gryphopsylla* *Pygiopsylla* *Cratynius*	2 = Australian Palaearctic	7	*Gryphopsylla* *Lentistivalius* *Pygiopsylla*	All Australian	–	—	—

* = The species of *Lentistivalius* in Malaya is a bird-flea, unlike other members of the genus.

C. Notes on the Fauna of Sumatra and Java as Compared with Malaya and Borneo

In the text above, it was noted on a significant number of occasions that certain mammals known from Malaya, Sumatra and Borneo had not been recorded from Java. This discrepancy is quite striking, as can be seen from Table 10, which lists the relevant distribution for many of the mammals we have been discussing (but is not to be considered a complete tally for all mammals). Of the 20 species or groups of mammals cited as occurring in both Malaya and Borneo, no less than 19 (95%) are likewise found in Sumatra, but only 8 (40%) of these are known from Java as well. All those listed for Java are known for at least Sumatra and Malaya. Insofar as concerns any of the hosts under discussion in this article and for which reasonable data exist, I know of no instance of a Javanese mammal which is present in Malaya or Borneo but which is unrepresented in Sumatra. (This is not to imply that there are no endemic Javanese rodents or other mammals, for there are, e.g. *Rattus* (*Maxomys*) *bartelsi*. Similarly, the leopard is absent from Sumatra and Borneo but inhabits Java, while wild oxen are unknown on Sumatra but occur in the other three areas. These mammals are not being discussed here.) There is one rat that is listed by Ellerman (1941) for Java and Borneo but not Sumatra, and that is *R.* (*Maxomys*) *eremoriventer*.[6] However, Ellerman had no Malayan record for this species either, and we now know it is abundant there. It therefore seems likely that it is present on Sumatra as well.

It is regretted that so little is known about Indonesian fleas that it is impossible to prepare comparable data on Siphonaptera for analysis.

The fleas of Malaya, Java and Borneo are analyzed further in Tables 11 and 12, but Sumatra is deleted therefrom because of the insufficiency of data. In Table 11 are listed the relevant fleas we have been discussing, showing the species known from Malaya, Java, Sarawak and Sabah. The data deal with non-volant hosts, but *Lentistivalius insolli* Traub, 1950, a bird-flea, is included because other members of the genus infest mammals. It is pointed out that *Stivalius jacobsoni* and its sibling new species are regarded as belonging to an unnamed genus, and *S. mjoebergi* and *S. klossi* are tentatively placed in another such genus.

Three of the species of *Medwayella* occur in both Malaya and Sarawak, but these are unknown in Sabah. Of the 5 *Medwayella* in Sabah, only 1 has been found in Sarawak. However, 5 *Medwayella* listed for Sarawak are unknown farther north. There are 18 species, representing 10 genera, known from Sabah, but only 2 of these are reported from Sarawak, where only a total of 8 species, including 7 *Medwayella*, have been recorded.

There are 10 relevant genera and 24 species of fleas occurring in Borneo (Sarawak and Sabah). Seven of these genera are also found in Malaya, the exceptions being the Bornean *Gryphopsylla*, *Pygiopsylla* and *Cratynius*, and the Malayan *Syngenopsyllus*, *Rothschildiana* and *Palaeopsylla*. The Malayan genera not reported from Borneo do occur in Java, however. Twenty-one of the Bornean species are unknown in Malaya, but at least 5 close relatives are found there instead.

[6] Oddly enough, this species is apparently not mentioned by Misonne (1969) and is not listed in his index. Since he cites Java as the southern limit of what he calls (*Maxomys*), and *R. eremoriventer* is common on Borneo, it is difficult to know where he would place this taxon.

Nine of the 10 Malayan genera occur in Java. Five Javanese species, representing 4 genera, are also found in Malaya. Seven of the 10 Javanese genera are found in Borneo. Three of the 14 genera represented in Table 11 are found in all 4 areas. However, if Sabah and Sarawak are considered as an entity, this figure is raised to 6.

Table 12 deals with the numbers of genera shared by Malaya, Java and Borneo, treating two of the areas at a time. The corresponding absentees are listed, and their apparent zoogeographic affinities indicated. For example, 9 of the 11 Javanese fleas are also found in Malaya, and the 2 that are unreported there are *Cratynius*, which is of Palaearctic ancestry (as noted in the Discussion below), and *Stivalius* (*s. str.*), whose origins are presumed to be in the Australian Region. The high correspondence of genera between Java and Borneo (7 of the 10 Bornean and 11 Javanese) and between Malaya and Borneo (7 of 10) is noteworthy. Three of the genera present in Malaya and Java but unknown in Borneo are of Palaearctic affinity.

III. DISCUSSION

A. Introduction

With the foregoing data and observations as a background, attempts are now made to answer, in sequence, the following major questions:

(1) Is the intimate association between fleas of the genus *Medwayella* and squirrels of the tribe Callosciurini a fundamental one, or are *Medwayella*-fleas really tupaiid-parasites secondarily infesting squirrels?

(2) Is *Medwayella* derived from stock with a Palaearctic origin or affinities?

(3) What are the geographic origins of callosciurine squirrels of the Malayan and Burmo-Chinese Subregions, and of their fleas?

(4) What are the geographic origins of the fleas infesting the subgenus *Rattus* and insectivores in those Subregions, and of those hosts?

(5) What are the zoogeographic inter-relationships of Malaya, Sumatra, Java, Sarawak and Sabah, and the Philippines, as indicated by the fleas and their hosts?

B. Callosciurines as the True Hosts of *Medwayella*

Callosciurines and tupaiids are not only the most common hosts of *Medwayella*-fleas, more so than those of any other groups of mammals, but their ranges roughly parallel that of this genus of Siphonaptera. Both callosciurines and tupaiids are found in all the countries and major islands of the Oriental Region, and both are absent from Luzon. These squirrels have a somewhat greater range, however, reaching Ceylon, Formosa, Celebes (Wallacea) and even to the fringes of the Palaearctic in the mountains of southern Asia, where there are no tupaiids. *Medwayella* has been found in all the areas where these two groups of mammals are both present, with the exception of India, where there has been little or no collecting of fleas in the relevant habitats. Further, except for Formosa, adequate data on fleas are lacking from those areas where callosciurines occur in the absence of tree-shrews. It may therefore be that *Medwayella* occurs there as well.

Analysis of the data, however, indicates that callosciurines, and not tree-shrews, are the true or characteristic hosts of *Medwayella*. Thus, in Malaya, where we have collected extensively, one species (*M. calcarata*) was never taken on *Tupaia*, and *M. limi* was rarely found on that host, and only 10% of the *M. dryadosa* came from *Tupaia*. It is true that 50% of the *M. phangi* there were from tree-shrews, but 49% came from callosciurines. Even if one considers only the fleas collected on *Tupaia* in Malaya, 80% of the records deal with but one species of *Medwayella*, but there are 6 species of *Medwayella* in the area (Traub, 1972a). In the few instances where *Tupaia* served as the major host for certain fleas, e.g. *Lentistivalius vomerus* and *Stivalius mjoebergi* on Mt Kinabalu in Sabah, there were no *Medwayella* found.

Another reason to minimize the possibility of a basic or original connection between tupaiids and *Medwayella* is that there is no correlation between the numbers of species of fleas and those of the host, nor are there any geographical or ecological features to account for such a discrepancy if there were such a relationship. For example, there are only 2 species of *Tupaia* in Malaya, and the only other tupaiid is *Ptilocercus*. None of these are known to harbour specific fleas, and it is unreasonable to expect that 6 species of local *Medwayella* could have evolved on tupaiid hosts (even extinct ones) and today exhibit so little evidence of such a relationship. It is true that there is a wealth of tupaiids on Borneo and that 3 species of *Medwayella* are currently known from these hosts, but there is little evidence of specificity in their relationships. Moreover, although 9 species of *Medwayella* are known from Bornean callosciurines, there are a number of such squirrels which have not yet been examined for Siphonaptera, and these may also be hosts of *Medwayella*. In contrast, sundry *Tupaia* there have been relatively frequently checked for fleas. As for the other tupaiids, neither *Dendrogale* nor *Urogale* has characteristic fleas, but nothing seems to be known about the ectoparasites of *Anathana* Lyon, 1913.

Like the tree-shrews, the numbers of species of *Medwayella* are at their maximum in Borneo, and decrease markedly according to the distance from the heart of the Malayan Subregion. This is true for callosciurines only with respect to the Philippines and Celebes, for these squirrels are well represented to the north of the known range of *Medwayella*. However, this apparent correlation between tupaiids and *Medwayella* is believed to be coincidental and an independent reflection of the geographic limits and centre of development of each group. Further discussion of this point, concerning *Medwayella*, will be presented below.

C. Origin and Affinities of *Medwayella*

Inasmuch as *Medwayella* is a pygiopsyllid, the distribution of the family is highly relevant. Two-thirds of the genera and 60% of the species of pygiopsyllid fleas of non-volant hosts are found in New Guinea or Australia, or both, and of these, one genus (*Pygiopsylla*) occurs in Borneo as well (i.e. *P. tiptoni*). Nearly 89% of the known species are found in the Australian, Wallacean or Oriental Regions, and 80% of the total number of species are found in the archipelagoes and islands of those Regions. It is my conviction that these figures imply more than the mere fact that the pygiopsyllids have reached the heights of development in that part of the world,

but rather that they arose in the New Guinea–Australian Subregion and from there extended west and north through the 'Malfilindo' Archipelagoes towards and into Asia (Traub, 1966; in press; in prep.). The occurrence of one endemic genus each in the Ethiopian and Neotropical Regions is regarded as evidence of ancient faunal links, via island-hopping mammal-hosts, between the Southern Continents, and hence serving in support of the theory of Continental Drift (Traub, in press; in prep.). The low number of pygiopsyllids on the Asian mainland, the dearth of Palaearctic species (only 1, a Japanese member of the wide-ranging *Lentistivalius*, which is believed to be a relatively generalized and ancient taxon) and the absence of Nearctic forms all reinforce this hypothesis of origin of pygiopsyllids in the Australian Region and militate against derivation from 'holarctic' fleas, with subsequent penetration south and east from the Asian mainland.

The affinities of the Bornean species, *P. tiptoni*, are also pertinent in this regard. The closest members of the genus, in both the geographic and taxonomic sense, are on New Guinea, and belong to a group associated with native murines, not the commensal species of the subgenus *Rattus*. The host of *P. tiptoni*, *Rattus baluensis*, may belong to the subgenus *Bullimus* according to Misonne (1969), who considers it most closely related to *R.* (*B.*) *xanthurus* of Celebes. Other data on fleas and mammals suggestive of faunal connections between New Guinea, Celebes and Borneo are discussed elsewhere (Traub, in prep.).

It is therefore hypothesized that the forebears of *Medwayella* originated in the Australian Region, but I believe that the genus itself arose in the Malayan Subregion (probably Borneo, where it is best represented) and became associated with callosciurines and travelled towards and onto the mainland as their squirrel hosts moved back and forth on their peregrinations, having penetrated the islands from the opposite direction (see below, p. 423). As has been noted above, the acme of evolution of *Medwayella* has been in Borneo (at least 11 species), and the number of species dwindles markedly toward the periphery of its range (1 species on Palawan, another on Mindanao, 2 in Indo-China). Of the other 4 genera or species-groups of pygiopsyllids represented on Borneo, 1 is endemic (*Gryphopsylla*), 2 include but 2 species (with only 1 reaching the continent), and 1 (*Lentistivalius*) is a wide-ranging taxon with 1 non-Asian species on the mainland. Insofar as concerns fleas of non-volant hosts and excluding *Medwayella*, only 6 species of pygiopsyllids are found on the continent, and 3 of these infest commensal rats.

The low number of pygiopsyllids in Asia militates against the possibility that the family (or even just *Medwayella* alone) arose on the continent. If the pygiopsyllids were indeed of Asian ancestry, one would have to postulate that their forebears were practically exterminated, probably along with their hosts, or else because of competition with other fleas. There is no evidence for such an origin. For example, no fossil marsupials have yet been found in Asia, and it is believed that pygiopsyllids were probably aboriginally associated with marsupials (Holland, 1969; Traub, 1968; Traub, in prep.). Further, the contemporary Asian pygiopsyllids certainly lack characters associated with primitive fleas such as possession of multiple combs of spines (Traub, 1968; 1972b) and as mentioned below, *Stivalius s. str.*, the taxon associated with *Rattus* (*R.*) *rattus* and which includes 3 species in Ceylon and India,

is rather specialized, suggesting geological youth. The relative dearth of Asian pygiopsyllids becomes more significant when it is realized that the most varied terrain on earth is found in the continental territory of the Oriental Region, i.e. habitats ranging from true desert, plains, swamps and equatorial rain-forest to mountain-deserts, coniferous forests, alpine meadows and subarctic scree and arctic wastes. Why did the aboriginal hosts of such theoretical pygiopsyllids, and/or the secondary hosts adopted by such pygiopsyllids as the original ones became extinct, fail to exploit such opportunity for radiation and evolution? The failure cannot be easily ascribed to 'competition', for there are vast areas of India, Thailand and Indo-China which have not been pre-empted by cricetids, or which are unsuitable for sciurids, and these should have been available for the hosts of Asian pygiopsyllids. (Incidentally, it is pointed out that no cricetid-pygiopsyllid is known.) In New Guinea there is an enormously diversified pygiopsyllid fauna infesting murids, and hence it would be expected that ancestral Asian pygiopsyllids, if there were any, would be associated there with murids, particularly since it is often claimed (as Darlington, 1957, stated) that murids '. . . have replaced most cricetids in tropical Asia and in Africa'. If this is so, it is strange that the murid fauna of the Indian Subregion and the South East Asian Mainland is so sparse. Thus, this huge and diversified area includes only 15 genera of murids, but there are 12 such genera in the Philippines alone, of which no less than 10 are endemic, while only 8 of the Asian ones are endemic. In New Guinea there are 22 murine genera, with 16 found nowhere else (Traub, in prep.). Moreover, the Asian murids which allegedly replaced the cricetids, and which undoubtedly are highly successful where they do occur, have failed to adapt themselves to the deserts or the upper reaches of the mountains of Asia. This is in contrast to what the murids have accomplished on the heights of the mountains of Africa and in the deserts of Australia. It is evidence of this type that makes me wonder (Traub, in press; in prep.) if, like the pygiopsyllids, the murids did not really have their origin, or early development, in the Australian Region, as mentioned below (p. 430).

There is another observation that seems to support the contention about the origin of *Medwayella*, and that is the fact that this genus is apparently essentially restricted to the foothills and lower parts of the mountains within its range, rather than on the upper reaches and mountain peaks. Thus, of the 21 *Medwayella* known to me, none are truly characteristic of the really temperate climes above 6000 ft elevation in the mountains of the Malayan Subregion. There have been no *Medwayella* taken at 4500 ft, or higher, on Mt Kinabalu, for example, even though squirrels are common in the area. In contrast, species of *Macrostylophora*, a ceratophyllid, are commonly found on callosciurines at such elevations, and as indicated below, that genus is of Palaearctic extraction. It seems fitting that a genus of New Guinean–Australian affinity should be restricted to relatively mild climes, rather than a temperate or near-alpine one, which is characteristic of ceratophyllids. Along these lines, it is of interest that, unlike the condition in the 'holarctic' regions, there is apparently no true alpine fauna of mammals, and virtually none for fleas, on the high mountains of New Guinea or on Mt Kinabalu. What happens is that as one ascends the upper levels of these mountains, the only

pertinent and faunal change noted is that fewer species of mammals are present, but no new kinds appear to replace them. This is also true of the fleas on Mt Kinabalu, and to a great extent, on the New Guinea mountains as well. The fact that there are a few distinctive alpine fleas in New Guinea, and that these are pygiopsyllids, supports my belief that the family has a more ancient history in the New Guinean and Australian Subregions than in the Oriental Region.

There are other indications that *Medwayella* is a relatively youthful taxon with roots in the Australian Region that became adapted to callosciurines in the Insular Malayan Area. *Medwayella* not only lacks primitive characters such as abdominal ctenidia, but is actually specialized in certain respects, e.g. the lumacaudate process, the structure of the aedeagus (Traub, 1972a) and the modifications of the pronotal comb in the manner of the fleas of tree-squirrels (Traub, 1972b). The generalized pygiopsyllids, in contrast, are all in the Australian Region, and not within the range of *Medwayella*.

D. Geographic Origins of Callosciurine Squirrels and Their Fleas

1. The Callosciurine Fleas

While the zoogeographic evidence indicates that *Medwayella* is descended from fleas of Australian–New Guinean origin, the data clearly indicate otherwise for the other callosciurine fleas and for the squirrels themselves. Considering the data on Siphonaptera first, it will be recalled that there are 3 other genera of fleas, *Macrostylophora*, *Syngenopsyllus* and *Paraceras*, all ceratophyllids, associated with these squirrels. (A fourth such genus, *Nosopsyllus*, occurring in India, is found on *Funambulus*, which is not in the Callosciurini.)

It is emphasized that the family Ceratophyllidae is definitely a northern one, for out of 31 genera[7] with species infesting non-volant hosts, 28 (90%) occur in the Nearctic or Palaearctic Regions, while 8 of these are truly Holarctic (Traub, in prep.). There are 316 relevant species in this family,[8] and of these, 252 (80%) occur in the Nearctic or Palaearctic Regions (including 6 which are literally Holarctic). There are no Neotropical ceratophyllid fleas of non-volant hosts, and no ceratophyllids at all in the Australian Region. Only 5 genera (16% of the total) occur in the Oriental Region, but only 2 (*Syngenopsyllus* and *Hollandipsylla*, with 3 and 1 species respectively) are endemic. The others (*Nosopsyllus*, *Paraceras* and *Macrostylophora*) have Palaearctic representatives and the first is mainly Palaearctic. There are but 2 Ethiopian genera: *Libyastus* (15 species) and *Nosopsyllus* (with only 1 of 46 species occurring there). It is noteworthy that even bird-ceratophyllids are absent from the Australian Region, despite the fact that some are notoriously far-ranging, e.g. *Dasypsyllus stejnegeri* (Jordan, 1929), described from the Arctic, is known from Mexico and the Falkland Islands, and *Dasypsyllus gallinulae* (Dale,

[7] This total includes *Ceratophyllus* Curtis, 1832, in which 45 of 46 species infest birds, but 1 Holarctic species, usually placed in this genus, parasitizes carnivores.

[8] The 2 *Nosopsyllus* and 1 *Monopsyllus* of commensal rats are included in these totals.

1878) is not only Holarctic, but has been found in Borneo, the Philippines and Malaya.

In the Southern Hemisphere, the majority of ceratophyllids are squirrel-fleas, but this is not so in the Northern one. In the Nearctic Region 6 out of 17 genera of ceratophyllids (35%) have some species of fleas that infest tree-squirrels (including flying-squirrels) or scansorial sciurids; in the Palaearctic, 8 of 18 genera (40%). The number of such species of squirrel-fleas in those Regions totals 81 of 196 (41%). In the Southern Hemisphere, by contrast, at least 14 of 15 *Libyastus*; all of the *Macrostylophora* (28 species, of which 26 are Oriental and 2 Palaearctic) and *Syngenopsyllus* (3 species); the monotypic Bornean *Hollandipsylla* and 6 of the 12 Oriental species of *Nosopsyllus*[9] infest squirrels. Only 1 of the 10 *Paraceras* is known to be a squirrel-flea (in Indo-China), but 3 of the species are Palaearctic. In all, 53 of the 64 (83%) Oriental and Ethiopian ceratophyllids are squirrel-fleas, 38 species in the former Region and 15 in the latter.

In so far as concerns the Oriental ceratophyllids of sciurids, virtually all in the Malayan and Burmo-Chinese Subregions are associated with the tribe Callosciurini. *Hollandipsylla neali* Traub, 1953, is the only exception, and it is known only from a flying-squirrel. In the Indian Subregion, the known squirrel-fleas are nearly all *Nosopsyllus*, on *Funambulus* (Funambulini) with but 1 *Macrostylophora* reported (from Ceylon, also on *Funambulus*). In the Palaearctic (Himalayan) region of West Pakistan, *M. fimbriata* and 2 monotypic new genera of ceratophyllids are associated with flying-squirrels. (No Callosciurinae are known to occur in the area.)

Except for *Medwayella*, the only squirrel-fleas associated with callosciurines anywhere, or occurring in the Malayan or Burmo-Chinese Subregions at all, are ceratophyllids. The points outlined above indicate that the Ceratophyllidae is a family that originated in the Northern Hemisphere, implying that the Oriental members were derived from Palaearctic roots. Further consideration of the genus *Macrostylophora*, and the data on squirrel-fleas in general, both strongly suggest that such an inference may be correctly drawn. *Macrostylophora* is the dominant genus associated with Callosciurinae, outnumbering the species of *Medwayella*, and having much broader geographical and ecological ranges than does that pygiopsyllid. Since 26 of the 28 species of *Macrostylophora* are found in the Malayan or Burmo-Chinese Subregions, and the bulk of these are endemic to an island, or a relatively restricted geographic area, like Malaya, it is logical to assume that many of these species actually arose there. Nevertheless, the morphological and taxonomic features of *Macrostylophora* clearly indicate Palaearctic origin. Thus, the two new genera of Himalayan (hence Palaearctic) ceratophyllids share some of the cardinal features of *Macrostylophora*, though otherwise abundantly distinct, and a redefinition of the last-named taxon is necessary as a result. Further, these (and other) new Palaearctic taxa also indicate the need for revision of the classification of such ceratophyllid genera as *Callopsylla* Wagner, 1934, and *Citellophilus* Wagner,

[9] The remaining Indian *Nosopsyllus* (6 species) infest murines and gerbillines, as do the Palaearctic species (33 species). The sole Ethiopian species is a murine-flea.

1934 (both Palaearctic), and the Holarctic *Monopsyllus*, none of which occur in the Oriental Region.

The data on squirrel-fleas summarized in Tables 8 and 9 (pp. 411 and 413), outlined above (pp. 414 and 422), also reinforce this contention of Palaearctic affinity. The third family of fleas associated with squirrels (but not Callosciurinae) is that of the Hystrichopsyllidae, and while squirrel-fleas are rare in the group, involving only 6 of 443 species, it is significant that this family too is common in the North. Thus, 74% of the known genera are found in the Nearctic or Palaearctic Regions. The 4 genera of hystrichopsyllids (3 Nearctic and 1 Holarctic) associated with squirrels also have species which infest peromyscines (Cricetidae), and this is also true of 5 of the ceratophyllid-genera (4 Nearctic and 1 Holarctic), which parasitize tree-squirrels. Moreover, in 7 out of these 9 genera, the species infesting tree-squirrels are in the minority (e.g. 1 of 23 *Kohlsia* and 2 of 52 *Rhadinopsylla*). This suggests that these genera are not only of northern origin, but that they originally were associated with cricetids, rather than sciurids. The hystrichopsyllids in question are nest-fleas, and this likewise indicates that the connection with squirrels is not primary. Inasmuch as 22% of the species of ceratophyllids infest tree-squirrels and the other sciurids under consideration, it would seem that there has been a long connection with such hosts even if their forebears had parasitized other mammals. The fact that at least 14 of the 16 Ethiopian ceratophyllids (15 *Libyastus* and 1 *Nosopsyllus*) are parasites of tree-squirrels also bespeaks of a basic and long-term association. The Palaearctic affinities of the Ethiopian species is clear from their morphology. Jordan (1936) when describing *Libyastus*, placed it near the Holarctic *Tarsopsylla*, and the single *Nosopsyllus* closely resembles the many Palaearctic members of the component subgenus.

The very great distance between the Ethiopian squirrel-fleas and the epicentre of *Macrostylophora*, coupled with the fact that ceratophyllid fleas occur on the equally remote squirrels in the Temperate Middle American Subregion, also argues for Palaearctic (or Holarctic) rather than Oriental origin of *Macrostylophora*. The dearth of other Oriental ceratophyllids points in the same direction. Squirrel-fleas account for 37 (76%) of the 49 species of Oriental ceratophyllids, and 31 (84%) of 37 in the Malayan and Burmo-Chinese Subregions. The preponderance of squirrel-fleas in the ceratophyllid fauna in the Oriental Region, together with the low number of taxa on various hosts, as compared to the Palaearctic, suggests an original entry from the North, and a relatively recent one at that.

2. Origins of Callosciurines

If the ancestral *Macrostylophora* are of Palaearctic origin, what of the aboriginal callosciurines? The Oriental Region and Celebes house so many kinds of sciurids compared to the rest of the world that it is easy to wonder whether the family could have arisen there. Thus, the Callosciurini (which barely extends beyond the Oriental Region into the periphery of the Palaearctic) includes approximately 13 genera and

48 species.[10] The great bulk of these are restricted to the S. E. Asian Mainland, the Insular Malayan Area and the Wallacean Subregion. Within their range are also found a few diurnal squirrels belonging to other tribes, as follows: (1) the monotypic and little-known *Rheithrosciurus* in Borneo, the only member of the tribe Sciurini in the entire Region, and with its geographically nearest relative in in the central Palaearctic; (2) the genus *Funambulus* (5 species), the only Oriental representative of the tribe Funambulini, which is otherwise African; (3) *Ratufa* (4 species), the only constituent of the tribe Ratufini.

The Oriental and Wallacean Sciurinae therefore total 16 genera and about 58 species, included in 4 tribes. The Petauristinae are also highly developed in the Oriental Region, with about 10 genera occurring therein (but many of these are also Palaearctic). In contrast, there is only a total of 5 genera of Sciurinae (excluding Marmotini) in Europe, Palaearctic Asia and the New World (in the classification of Simpson, 1945), but these apparently comprise 42 species. The Marmotini would add 4 genera (6 genera fide Moore, 1959), if one wanted to include marmots, spermophiles and chipmunks. None of the other Regions include more than 3 tribes of Sciurinae, with a maximum of 6 genera per tribe occurring in the Nearctic Marmotini. There is only 1 genus (2 species) of flying-squirrel in the New World. The contrast in wealth of fauna, at the generic and tribal levels, is quite striking, especially in view of the far greater land-surface and type of habitats represented in the Eurasian Palaearctic and Nearctic areas as compared to the Malayan and Burmo-Chinese Subregions and Wallacean Subregion, where the bulk of the callosciurines occur.

The fossil record is of little assistance in trying to determine whether the diversification of sciurids in the Oriental Region is due to rapid adaptation by the descendants of immigrants to a superb environment for arboreal forms or to an ancient history of autochthons. Very few fossils of any mammals are known from the Malayan and Burmo-Chinese Subregions, and there are no such sciurids. Fossils are known from the Oligocene to Recent in Europe and North America; from the Pleistocene to Recent in Asia; and from the Pleistocene in South America and the Pliocene in Africa (Simpson, 1945; Anderson & Jones, 1967; Cooke, 1968; Patterson & Pascual, 1968). Walker et al. (1968) state that ground-squirrels are known to date from the late Miocene, 'whereas the tree squirrel extends back in time possiby to the Oligocene'.

If there is a specific account of the origins and migrations of the sciurids in general, it has escaped my notice. Since the family is absent from the Australian Region, it has not been mentioned by Simpson, Tate, etc., when discussing the origins of the Australian fauna, as mentioned regarding murids below (p. 430). It is regretted that Moore & Tate, in their fine opus on Sciurinae of the Indian and Indochinese

[10] Moore (1959) in his revisionary work on the higher classification of the Sciurinae mentions 12 genera and 6 subgenera of Callosciurini. One of his subgenera, however, namely *Tamiops*, is here treated as a genus, following Moore & Tate (1965) and Harrison (1966). In the absence of any single authoritative source, the figures for the numbers of species is based upon an analysis of a variety of references, including Ellerman (1940), Ellerman & Morrison-Scott (1951), Harrison (1968), Laurie & Hill (1954), Medway (1963), Moore (1958 & 1959), Morris (1965) and Walker et al. (1968).

Subregions (1965) did not deal with zoogeography beyond the presentation of interesting and original ideas concerning elements of the local fauna. However, elsewhere Moore did discuss aspects of the zoogeography of certain groups of squirrels, i.e. Neotropical, Nearctic and northern Palaearctic diurnal squirrels (1971b) and those of the Indian Subregion (1960). In the first article, the 'probable place of origin is shown to be the Nearctic Region for the (subtribes) Tamiina, the Spermophilina and the Marmotina'. The subtribe Sciurina, in Moore's opinion, could have arisen in either the Palaearctic or Nearctic, but the Palaearctic is stated to be the 'centre of dispersal'. In the 1960 paper, Moore reiterated (p. 5) that *Funambulus* 'has African affinities', a point first made by him in 1959. Moore (1960) also regards the Indian habitats of *Ratufa* as an extension of its range from what is here called the Burmo-Chinese Subregion.

Matthew (1915), in an enormously influential opus, expressed the view that the 'Holarctic' area was the epicentre of origin of the dispersal of vertebrates, and pointed out that while great radiation and expansion has occurred in the southern continents, the aboriginal types were invaders from the north. He summarized his theories along similar lines in 1930. Darlington (1957, pp. 488–489) considered Sumatra, Java and Borneo as 'zoogeographically . . . very recent continental islands . . . that were all connected together and to the mainland in the Pleistocene'. He clearly regarded the fauna as 'a nearly complete continental one' and including a 'rich Oriental mammal fauna', which shows the 'beginnings of the effects of isolation and limitation of area', and with extinctions resulting in a relict pattern. Darlington (1957, p. 503) believed that the Philippine mammals (except the murids) arrived via 'rather recent immigration from Borneo'. Raven (1935) also indicated that the Philippine fauna was derived from that of 'Malaysia', and Taylor (1934) had expressed similar ideas. The sciurids of the Ethiopian Region are considered by Cooke (1968) as having been of Palaearctic origin, derived from Europe, presumably in the late Oligocene.

It should be noted that while Darlington (1957) concurred with the idea that the fauna of the Australian Region and Malfilindo Archipelagoes were derived from Asia, he did not state that they necessarily arose in the Palaearctic. In fact, in 1959 he clarified and expanded this point, claiming that the 'main Old World Tropics (tropical Asia and Africa)' was the place of origin for many dominant groups of animals, including the mammals, and that from there they dispersed in all available directions. Thus in the case of murids, Darlington believed they penetrated into Australia via the Pacific Islands. Squirrels are regarded by him as another dominant group that arose in the 'Old World tropics' and dispersed from that centre, although Darlington refers only to this group in passing, and does not give particulars as to where he believes the various taxa arose. This is an interesting and impressive hypothesis, and the wealth of callosciurine fauna on the South-East Asian Mainland at first glance appears to render it solid support. However, as Darlington himself points out, it is difficult to define what constitutes the Old World tropics, and the geographic areas encompass a tremendous diversity of habitats, including deserts, a variety of forests, alpine terrain, mangrove swamps, etc. Moreover, the upper reaches on the mountains in Asia are often Palaearctic, rather

than Oriental. Did the squirrels arise in the temperate or the tropical parts thereof?

In view of the dearth of information on fossil sciurids, and the complete absence of records of fleas of critical squirrels like the sole member of Sciurini in the middle of Borneo, and of Celebes squirrels, it is futile to try and decide definitively here whether sciurids actually arose on the mainland of the Oriental Region, or whether they radiated there rapidly after the arrival of aboriginal forms from the north. However, the data on Siphonaptera, outlined above, do suggest certain relevant conclusions, particularly: (1) the number and diversity of ceratophyllid fleas parasitizing squirrels indicates that the basic association is an old one, and that it reached its height at the generic level in the Palaearctic and Nearctic Regions; (2) the bulk of the fleas of Oriental squirrels are definitely of Palaearctic origin; and (3) the squirrels of the Insular Malayan Area and Wallacea were derived from forms that entered from the Asian Mainland; and (4) their entry there was comparatively recent, geologically speaking.

Thus, the Ceratophyllidae, the main family of fleas which is associated with squirrels throughout their range, clearly had its roots in the Northern Hemisphere, as we have seen. More than 50% of the genera in the family include species infesting relevant squirrels, and 41% of the species in those genera actually parasitize such hosts. However, 61% of those genera are found in the Palaearctic or Nearctic Regions, even though a small proportion of the genera of squirrels dwell there, e.g. more than two-thirds of the Sciurini are found in the Oriental and Wallacean Regions. Moreover, some of these genera are quite specialized, at times monotypic, and restricted to squirrels. Only 31% of the ceratophyllid genera with squirrel-fleas inhabit the Oriental Region, despite the wealth of hosts. Since there are so few ceratophyllids at all in the Insular Malayan Area, and these are comparatively of little diversified at the generic level, it would appear that the entry thereto by squirrels was in relatively recent geological times, and that only a few pioneers were involved. (Of course the period must have been long enough to permit the local development of a large number of species within these few genera, as the squirrels radiated within the Region.) It is pointed out that if these migrant-hosts from the north were not sciurids, then they left no trace behind in the Oriental Region in so far as concerns fleas, for *Macrostylophora*, *Syngenopsyllus* (and *Hollandipsylla*, the petauristine flea from Borneo), which are kin, have no near allies in the Region (although they do in the Palaearctic, on squirrels). The fourth genus of ceratophyllid in the Malayan Subregion, *Paraceras*, which is occasionally (1 species) associated with sciurines, is not closely related to these other ceratophyllids. It is reiterated that not all the Oriental squirrel-fleas are of northern affinity, and I believe that on these islands, probably Borneo, the squirrels, working their way south and east from the mainland, encountered *Medwayella* or its prototype, which had migrated (with other pygiopsyllids) in the opposite direction, from Celebes or the Australian Region, and that *Medwayella* then accompanied the callosciurines as they moved back and forth between the mainland and the islands, and towards Palawan and Mindanao.

Zoogeographic data on the sciurid-fleas of Formosa may also provide a possible clue about the origin of the squirrels. Both diurnal squirrels (callosciurines) and flying-squirrels (*Petaurista*) occur on that island, and the former harbour *Macrostylophora* but the latter are infested with *Monopsyllus argus* (Rothschild, 1908), a Palaearctic flea which is found as far east as Japan, where it is also found primarily on *Petaurista*. The most common *Macrostylophora* is *M. liae*, also known from Fukien on the Chinese mainland. In both areas this flea is associated with *Tamiops swinhoe* and *Callosciurus erythraeus* (Pallas, 1779). The Formosan callosciurines and their fleas are of Oriental affinity, but what is the significance of the Palaearctic species of flea on *Petaurista*? These giant flying-squirrels range from Kashmir and Szechuan to Borneo and the Far East, and are usually found in the mountains of the Oriental Region but also occur in the foothills, as low as 1500 ft elevation, as in Malaya. In Pakistani Kashmir (in the Palaearctic Region) a new genus of ceratophyllid of Palaearctic affinity is found on *Petaurista*, while a second such new genus parasitizes *Hylopetes* in the same area. No characteristic fleas have been found associated with any flying-squirrels in Malaya, and within the last few years these hosts have been intensively studied, and examined for fleas, by the U.S. Army Medical Research Unit (Malaya). It may be significant that these USAMRU collections were primarily from the lower elevations. The only petauristine-flea known from the Oriental Region is *Hollandipsylla*, a ceretophyllid of Palaearctic ancestry collected in the truly cool climes of Mt Kinabalu. The available data therefore suggest that the flying-squirrels entered the Oriental Region from the north, bringing their stocks of Palaearctic fleas with them, and that in the tropical areas they lost their fleas and have not yet become affiliated with Siphonaptera of native origin. In the Himalayas, however, where the Palaearctic merges with the Oriental Region, *Hylopetes* has acquired *Macrostylophora fimbriata*, which of course is a member of an Oriental genus (associated with callosciurines) and is of northern ancestry, and has transported it to Pakistani Kashmir, where callosciurines are unknown.

The apparent absence of callosciurines in that part of the Himalayas, where at least 3 genera of petauristines occur, is a fascinating problem. Perhaps the callosciurines became extinct there, but it seems more likely they were never present, due to one or more of the following possible factors: (1) the callosciurines are too youthful a group to have yet penetrated; (2) the available habitats are themselves of such recent derivation that only the more mobile petauristines could successfully exploit them following extinction of the original fauna; and (3) the petauristines entered from the Palaearctic climes of the northern and eastern branches of the Himalayas and hence were adjusted to the rigorous climes, unlike the callosciurines, which as a group are associated with far milder climates.

If (3) were the answer, it would not explain why callosciurines were absent from the forest in the lower elevations of these particular areas in Kashmir. (The occurrence of *Funambulus* in the plains just a few miles away is attributable to the African origins of funambulines. The faunal connections between the arid areas of West Pakistan, and the deserts of Iran, leading to North Africa, are reasons for placing this part of the Indian Subcontinent in the Southeast Palaearctic Subregion.) If the second factor above was the reason, then the 'ecological islands'

in the mountains of Gilgit, Dir, etc., scattered throughout the deserts of Central Asia must have become isolated a relatively short time ago.

Various of the points made above indicate that the sciurids in the Insular Malayan Area were relatively recent immigrants. As mentioned elsewhere (Traub, in prep.), I believe that in certain parts of their range they entered into competition with sundry giant tree-rats which had entered earlier, moving from a New Guinean focus, and that, as a result, the tree-rats became extinct in certain areas. It is striking that the giant tree-rats have reached the apex of their development in areas where squirrels are unknown (New Guinea, Flores, Luzon). Moreover, there are only a few regions where the two both occur, e.g. Mindanao and Celebes, but I have no data if they actually co-exist in the same micro-habitats.

E. Geographic Origins of *Rattus*-Fleas and Their Hosts

1. *Rattus*-Fleas

There are five families of fleas associated with rats of the genus *Rattus* in the Oriental Region, namely the Pygiopsyllidae, Leptopsyllidae, Pulicidae, Hystrichopsyllidae and Ceratophyllidae, and the first three of these occur in the Australian Region as well (and probably in the Wallacean). If the margins of the Palacarctic Region, such as the southern U.S.S.R., are added (and where pygiopsyllids are absent), this territory encompasses the geographic limits of the wild (non-commensal) members of the genus *Rattus*.[11]

As we have seen, the Pygiopsyllidae is overwhelmingly a family of the Southern Hemisphere, with the preponderance of genera and species (especially endemic ones) in the Australian Region, but with fair representation in the Insular Malayan Area. At least 16 of the 28 genera infesting mammals in the Australian Region are prime parasites of rats. Notably, 15 of these are restricted to New Guinea, where they parasitize a variety of murid genera but only relatively few of these are found on the genus *Rattus* (Traub, in prep.), and those that do so are invariably associated with subgenera other than (*Rattus*). It is worth emphasizing that Laurie & Hill (1954) and Lidicker & Ziegler (1968) do not list any native members of the subgenus *Rattus* on New Guinea—only commensal forms are known. The sixteenth genus of rat-pygiopsyllids of New Guinea, *Metastivalius* Holland, 1969, is also found in Australia, and includes a few species infesting the subgenus *Rattus*, but most of the members occur on other kinds of rats.

Similarly, all but one of the murid-pygiopsyllids listed in Tables 4 and 7 (pp. 402 and facing page 406) are parasites of true forest-rats rather than of the subgenus *Rattus*. Moreover, the records from the subgenus *Rattus* pertain to wild forms of (*Rattus*) occurring in secondary forest, and not from commensal rodents or species of rats typical of the grasslands, indicating these fleas had strayed from their proper hosts. The exception is *Stivalius* (s. str.), such as *S. cognatus*, and these characteristically infest the subgenus *Rattus* and usually are associated with subspecies of *R.* (*R.*) *rattus*.

[11] Misonne (1969), unlike earlier workers, does not consider the genus *per se* to be represented in Africa, and has raised the older 'subgenera' to full generic level.

The degree of specialization exhibited by the sundry pygiopsyllid rat-fleas is also of relevance. Many of the New Guinean murid-fleas are highly modified with respect to the shape of the head, and the development of helmets or crowns of spines or spiniform bristles which are apparently tailored to fit the nature of the hairs of the host (Traub, 1968; 1972b). Such adaptations suggest a long evolutionary history on these particular hosts, and seem to imply the groups are relatively ancient. The bulk of the pygiopsyllids of the forest-rats of the Indo-Malayan area (*Gryphopsylla* and *Stivalius s. lat.*), on the other hand, are much more generalized, and seem to have a younger history. (It is pointed out, however, that they lack the primitive features seen in some of the Australian and New Guinean pygiopsyllids, especially those associated with marsupials.) The fleas of *Stivalius* (*s. str.*) are quite distinctive in the family in that the sclerotized inner tube of the male is elongate, while the genitalia of the female are correspondingly modified (Traub, 1972a). A specialization of this type does not imply antiquity but merely a development that occurred subsequent to the association with *R. rattus*, since it does not occur in related taxa.

There are, then, four points about the pygiopsyllids of rats in the Insular Malayan Area that are in accord with the concept of the origin of the Pygiopsyllidae in the Australian Region and subsequent movement with their hosts through the Malfilindo Archipelagoes towards Asia. These are: (1) the relatively small number of such rat-fleas in the area, i.e. far less than in the Australian Region; (2) the progressive decrease in the number of pygiopsyllids on rats towards the periphery of the Oriental Mainland of Southeast Asia, and the absence of these fleas in the adjacent Palaearctic; (3) the close association of the bulk of the rat-pygiopsyllids of the Insular Malayan Area and the adjacent mainland with forest-rats rather than the subgenus *Rattus*, paralleling the case in New Guinea; (4) the significantly lower degree of specialization in the fleas of these forest-rats as compared with those of New Guinea.

As a corollary to this hypothesis, it might be suggested that *Stivalius* (*s. str.*) had a similar focus of origin and path of migration, and that the same is true of their characteristic hosts, *R.* (*R.*) *rattus*. Before dealing with this possibility, it is necessary to review the data on other fleas of the subgenus *Rattus* and of the rats themselves. The Leptopsyllidae on rats are instructive in this regard. The family is primarily a northern one, and of the 19 genera known, 16 (84%) occur in the Palaearctic or Nearctic Regions, with 4 of these truly Holarctic, 15 genera in the Palaearctic and but 5 in the Nearctic (Traub, in prep.). There are no Neotropical forms and only 2 genera occur in the Ethiopian Region, with 1 of these Palaearctic and the other endemic for Madagascar. There are 5 Oriental genera but only 1 is endemic (*Cratynius*). As noted in Section II.B.4 above, the leptopsyllids associated with rats are mainly in the subfamily Leptopsyllinae, especially in *Leptopsylla*, *Sigmactenus* and *Peromyscopsylla*. The other genera of leptopsyllids infest primarily cricetids, with a few exceptional species in the subfamily Amphipsyllinae attaching to rats in the Southeastern Palaearctic Subregion. Seventeen of the 18 species of *Peromyscopsylla* infest Palaearctic or Nearctic cricetids, but the single exception is a Palaearctic rat- or *Apodemus*-parasite which (or an undescribed sibling thereof) has been recently found in the mountains of Luzon on rats of the subgenus *Rattus*, accompanied by another Palaearctic leptopsyllid, a *Frontopsylla*

Wagner & Ioff, 1926 (Amphipsyllinae). Ten of the 15 species of *Leptopsylla* are known from murines, and about 3 of these are known from rats in the Ethiopian and Palaearctic Regions. A derivative of *Leptopsylla* (*Pectinoctenus*), namely *Sigmactenus*, is of especial interest because the 3 species extant are found on the genus *Rattus* in Borneo, New Guinea and the Philippines, respectively, with at least the last one infesting the subgenus *Rattus*. It appears definite, then, that faunal extensions of this predominantly northern family, which largely parasitizes non-murids, exist in the Malfilindo Archipelagoes and New Guinea, and that they are associated with *Rattus* or (*Rattus*). (A leptopsyllid of insectivores on Borneo and Java will be mentioned below.)

Another family which is well developed in the Northern Hemisphere but which has exceptional representation in the Insular Malayan Area is the Hystrichopsyllidae. Only 4 genera (9% of the total) are found in the Oriental Region and 3 of these are better known in the Palaearctic, namely *Palaeopsylla* (Ctenophthalminae), *Neopsylla* (Neopsyllinae) and *Stenischia* Jordan, 1932 (Rhadinopsyllinae). The fourth, *Rothschildiana* (a neopsylline) has been reported only in Malaya and Java, on *Rattus*. Eighty-two per cent of the genera of Neopsyllinae are restricted to the northern regions, and these taxa include 65% of the species. Of the *Neopsylla* for which we have information, 9 species (31%) are Oriental, with 3 (10%) in the Malayan Subregion (1 each in Malaya, Java and Borneo). Eight (89%) of the Oriental species infest *Rattus* (of several subgenera, including the subgenus *Rattus*), and the 7 Palaearctic members of the *N. stevensi*-group apparently parasitize the subgenus *Rattus*. While both *Rothschildiana* are *Rattus*-fleas, the bulk of the few available records are from the subgenera *Lenothrix* and *Maxomys*.

Palaeopsylla is mentioned below (Section F.1), since the genus is characteristic of insectivores. The precise hosts of *Stenischia* are in doubt since there have been relatively few reports, and while some species have been collected on insectivores (in Japan, Formosa, Nepal), I have some specimens from rats, not only in Formosa but for a new species from Thailand (1 specimen!), the only Oriental record for the genus.

From the foregoing it is clear that the Oriental hystrichopsyllids have Palaearctic roots and that most of the species involved are associated with *Rattus*, and often the subgenus *Rattus*. However, the zoogeography of the Hystrichopsyllidae in the Malfilindo Archipelagoes and the Australian Region cannot be explained by that concept alone, for 2 endemic genera, each representing distinct tribes, are found in Australia, infesting marsupials. There are no known hystrichopsyllids on New Guinea nor anywhere in the Malfilindo Archipelagoes save Java and Borneo. Such a discontinuous distribution is difficult to explain on the basis of hosts, for cricetids and insectivores, and not rats, are the major hosts of hystrichopsyllids in the Northern Hemisphere, and cricetids are apparently absent in the Malayan Subregion and the rest of the Austral-Asian Archipelagoes, while insectivores are poorly represented in that Subregion and Wallacea, and absent (except for commensal shrews) in the Australian Region. Moreover, endemic subfamilies or tribes of Hystrichopsyllidae are also found in South America and in Africa, separated by thousands of miles from their nearest relatives and 'expected' hosts. A distribution of this type, in my view, is evidence of aboriginal faunal 'island-hopping' connections

between the Southern Continents and renders further support for the theory of Continental Drift (Traub, in press; in prep.). Those who do not accept the hypothesis tend to explain the phenomenon in terms of original continuous distribution, followed by extinctions to create the gaps, and evolutionary changes to account for the phylogenetic modifications.

The Ceratophyllidae, a northern family as noted above, is primarily represented in the Insular Malayan Area by squirrel-fleas, but there also are data suggesting both a connection with rats and a Palaearctic origin therefor. The genus *Paraceras* includes Palaearctic and even European forms, but 7 of the 10 species occur in the Oriental Region, and 2 of these (both undescribed) presumably infest rats (Thailand, Malaya). The Malayan species is known only from about 6000 ft elevation, where it is common on *Rattus* (*Stenomys*) *bowersi* and *R.* (*Leopoldamys*) *edwardsi* (Thomas, 1882). A Bornean species infests the ferret-badger, *Melogale* (*Helictis*) *orientalis everetti* (Thomas, 1895). Another species associated with carnivores such as viverrids and (*Helictis*) Gray, 1831, is found in the Oriental parts of Formosa.

The Pulicidae, more than any other group of fleas, has a discontinuous distribution among the Southern Continents, and is rather poorly represented in the north. Thus, among the Xenopsyllinae, 78% of the 88 species are found in the Ethiopian, Oriental or Australian Regions; 78% of the 23 species of Pulicinae are known from the Neotropical, Australian or Ethiopian Regions; 73% of the 11 Archaeopsyllinae are from the Ethiopian or Oriental Regions (Traub, in prep.). The broad but discontinuous range even exists at the generic level: *Echidnophaga* Olliff, 1886, includes 6 endemic Australian species (on marsupials), 5 in the Ethiopian Region and 5 in the Palaearctic (Southwestern and Eastern Subregions). *Xenopsylla* is the most widely dispersed genus in the family, but, notably, there are no representatives in the New World. There are no less than 43 endemic Ethiopian species on gerbillines and murids, and 20 mammal-*Xenopsylla* are indigenous to the Palaearctic. In Australia there are 2 species (*X. vexabilis* and an allied form) associated with rats of the subgenus *Rattus*, and *X. vexabilis* is also known from New Guinea, Java, the Philippines (all on the subgenus *Rattus*) and from the Oriental Mainland of Southeast Asia, where it infests *R.* (*Bullimus*) *berdmorei*. (*X. cheopis* (Rothschild, 1903) and other species of fleas of commensal rats have been transported to many parts of the world and are ignored herein. *X. vexabilis* belongs in the synanthropic category, at least in part, and has been introduced into Hawaii, for example, but it may also be indigenous in parts of its known range and hence is treated as being relevant.) On the basis of the range of *X. vexabilis*, it would be easy to conclude that this species represents an original entry from the Palaearctic or Indian Subregion into the Oriental Mainland of Southeast Asia and hence into and throughout the Austral-Asian Archipelagoes, primarily via the subgenus *Rattus*.

Supporting this theory is the fact that a related species, *X. nesiotes* (Jordan & Rothschild, 1908) occurs on rats of the subgenus *Rattus* on Christmas Island, south of Java. However, the occurrence of a highly modified and endemic species of *Xenopsylla* on an autochthonous rat in New Guinea and another such from the mountains of New Guinea complicates the zoogeographic picture. Such indigenous specialized forms suggest antiquity, and since other pulicids (*Echidnophaga*) are

known in Australia, and share a common distribution at the generic level with Africa, it may be that these *Xenopsylla* have their roots in the Australian Region. It should also be noted that the affinities and hosts of the Palaearctic *Xenopsylla* (and even the Indian ones) indicate the possibility that the movements of the aboriginal *Xenopsylla* (and their hosts) were from Africa towards India, and not the reverse (a direction counter to the belief of virtually all mammalogists). Moreover, there are no endemic *Xenopsylla* known in Malaya, Burma, Tibet and China, so that no northern or western links for the Thai and Indo-Chinese *X. vexabilis* are apparent. Regardless of where *X. vexabilis* or its forebears originated, it seems to have accompanied commensal rats over much of their peregrinations. Thus, in New Guinea it has only been found in a few coastal areas, always on the subgenus *Rattus*. The Philippines records are also from commensal rats, in Central Luzon.

Regardless of such problems, however, on the whole the data on Siphonaptera strongly suggest that, with the exception of the pygiopsyllids (and perhaps the pulicids as well) the fleas infesting rats of the genus *Rattus* of the Australo-Asian Archipelagoes and the Oriental Mainland of Southeast Asia were derived from Palaearctic stocks. The evidence is strongest in the case of fleas infesting certain groups of *Rattus* and the subgenus *Rattus*. The low numbers of fleas involved at the generic and species level for all of the families in the Insular Malayan Area, suggest relatively recent entry. The relative wealth of mainland and Palaearctic taxa in the case of the hystrichopsyllids, leptopsyllids and ceratophyllids supports this view of youth, and the same is true for the pygiopsyllids when considering New Guinea as the possible ancestral homeland.

2. Geographic Origins of the Australo-Asian Murids and *Rattus*

The question of the origin of rats is being treated at length in the article dealing with fleas and Continental Drift (Traub, in prep.), and this subject will at present essentially be limited to relevant highlights. Practically all of the leading naturalists and mammalogists believe that the rats arose on the Asian mainland and then penetrated the various members of the Australo-Asian Archipelagoes, including Australia and New Guinea, progressing by rafts or 'island-hopping'. Simpson as early as 1940 could confidently state that it 'is generally conceded that . . . (the) . . . Australian rodents are of Asiatic origin and reached Australia without a continuous land-bridge' (p. 763). In 1961 Simpson elaborated on this point, and based upon the data of Tate (1936, 1951) and others, postulated that the rodents of the Australian Region could be divided into 4 groups, with different histories. One such group, the 'Old Papuans', include genera whose forebears are supposed to have reached New Guinea by multiple invasions from the East Indies in the period from the Miocene to the Pliocene. Another group, the 'Old Australians', are thought to have been derived from perhaps a single immigrant in the Miocene. A third group comprises the hydromyine rats, which Simpson believes evolved in New Guinea from an Asiatic ancestor in the Miocene, with later descendants moving to Australia and the Philippines. The fourth group is the one with which we are presently concerned, and this includes 'local members of the very widespread genus

Rattus'. A batch of autochthonous *Rattus* are believed to be derived from one or two migrants 'through the East Indies' in about the early Pleistocene. Much later, commensal rats entered in several waves, through the activities of man.

Asian ancestry of the murids (and all other indigenous mammals) of various parts of the Australo-Asian Archipelagoes was also proposed or accepted by Taylor (1934) for the Philippines; by Raven (1935); Darlington (1957; 1959) and Keast (1968; 1969). Misonne (1969) in a major and highly significant opus on 'African and Indo-Australian Muridae' also concurred regarding the Asian origin of these rats, particularly concerning 'Southeast Asia', but he seems to include Borneo and the neighbouring islands in 'Southeast Asia'. Nevertheless, he clearly agrees that the route of travel was towards the Australian Region, etc. However, there has not been complete unanimity on this score, for Ellerman (1940 and 1941) suggested that the rats arose in the Australian Region and migrated towards the Asian mainland, and that they 'are among the most archaic of mammals'. These ideas of Ellerman's were very strongly criticized by Simpson in 1945, and since Ellerman offered no rebuttal when (1949) referring to Simpson's opus, perhaps he had come to accept Simpson's views.

It is also the concensus that African mammals were derived from Asian or European stocks (Darlington, 1957; Cooke, 1968; Keast, 1969). Misonne (1969) also believes that the African murids are descended from Asian taxa.

The data on Siphonaptera, and a review of the zoogeography of mammals, have led me to seriously question whether the murids arose in Asia, or even the adjacent islands or underwent their major evolution there. In fact, I believe that their origin, or at least their aboriginal development as such, may have been in the Australian Region (Traub, in press; Traub, in prep.) and that this is where they acquired their pygiopsyllids and that they then moved, together with their fleas, via Celebes towards the Philippines, and in another line, towards Borneo and the mainland. According to this hypothesis, evolution of new forms continued through the eons as the murids moved back and forth between the islands, but progressing towards the continents, resulting in giant tree-rats and other endemic forms of ancient lineage in Celebes, Flores and the Philippines, etc., and the subsequent development of the genus *Rattus*. Various subgenera of *Rattus* appeared on some of the islands, probably including Borneo, and also on the mainland, and these migrated eastward to New Guinea, as well as westward and northward. This theory would account for the relative sparsity of murid genera on the Asian mainland, alluded to above (p. 422). As a corollary to this hypothesis, it is suggested that the African murids were also derived, to a great extent, from island-hopping stock from the Australian Region before the continents drifted too far apart. This would explain how the pygiopsyllids entered Africa, for there is no trace of the family in the Palaearctic Region between India and central Africa. Similarly, it is my belief that there were limited faunal exchanges of marsupials, complete with stephanocircid helmet-fleas and pygiopsyllids, and some hystrichopsyllids, between Australia and South America. Evidence from the Siphonaptera and their hosts also has led me to believe that the murids (and indeed most groups of rodents and insectivores) are a more ancient group than is generally believed, and that the rats were in New Guinea at

far earlier times than postulated by Simpson. These are all highly controversial points, and the data and arguments are being presented and developed elsewhere (Traub, in press; Traub, in prep.). They are mentioned here to emphasize that the Siphonapteran data nevertheless do strongly support Simpson's views (1961) about the relative ages of the various rats in his 'groups' of Australian and New Guinean murids and, particularly, that the *Rattus* group was the youngest, and that it entered the Australian Region from the western islands. Thus, the hystrichopsyllid and leptopsyllid fleas infesting rats in the Insular Malayan Area are obvious extensions of the Palaearctic Region, as we have seen, and as has been noted for the squirrel-fleas, etc. Further, they seem to be relatively recent evolutionary phenomena, e.g. *Rothschildiana* is a development of *Neopsylla*; and there has been little differentiation at the generic level in general, and little speciation. There is also a close association with the subgenus *Rattus*, as in the case of *Sigmactenus*, which has ranged as far east as New Guinea. Moreover, regardless of where the pulicid *Xenopsylla vexabilis* and the pygiopsyllid *Stivalius s. str.* actually arose, there can be no doubt that they are intimately connected with the subgenus *Rattus*, and probably *R.* (*R.*) *rattus* at that. They have been found together with (*Rattus*) in widely separated areas, and the species of *Stivalius s. str.*, at least, have differentiated at the subspecies level in a classical geographical manner. (Names for subspecies of *X. vexabilis* exist but their validity is in some doubt.) The degree of phylogenetic changes suggests geological youth for these taxa of fleas, indicating that their hosts are either young themselves or new in the areas. The fact that the species of *Stivalius s. str.* have specialized genitalia of a type not seen in related forms, and are restricted to *R.* (*R.*) *rattus*, makes me believe the taxon and its host developed together, even though the *Stivalius* are the descendants of fleas that originated in the Australian Region.

F. The Origins of Insectivore-Fleas and Insectivores of the Insular Malayan Area

1. Shrews and Shrew-Fleas

In many parts of the world, shrews (Soricidae) are abundant in numbers of individuals and species (and the scientific names proposed for them). This is true of the Northern Hemisphere in general, but not in parts of the far north. (Shrews even occur, to a limited extent, in the desert.) Several genera are endemic to the Ethiopian Region and the same is true for Ceylon. Soricids are poorly represented in the islands of the Malayan Subregion, but extend as far as Celebes. Native or wild forms are absent in Australia, New Guinea, and adjacent islands, all of South America save for the Nearctic extension therein; although the commensal *Suncus* Ehrenberg, 1833, has been introduced into some Pacific islands. *Crocidura* is probably the sole genus occurring in native form in the Wallacean Subregion, but its range extends northward to the Philippines and westward to and over much of the Palaearctic (but apparently not very far north in Asia) and thence deep into Africa. It is difficult to estimate the number of species in the various areas, for the genus is in sore need of revision. As Ellerman & Morrison-Scott (1951) point out, 110 names at the purported species level have been proposed for Africa alone.

Medway (1963) lists 2 species of *Crocidura* and 2 non-commensal *Suncus* for Borneo, and 1 of each of these also occurs in Malaya (Harrison, 1966). A third genus of soricid, *Chimarrogale* Anderson, 1877, a water-shrew, is found on Borneo, and Malaya and Sumatra, and may be represented thereon by various subspecies of a single species that is Palaearctic, extending as far as Japan, Szechuan and Kashmir.

Unfortunately, the only available data on fleas of soricids of the Malayan Subregion concerns *Crocidura*, and little information is available there, i.e. the occurrence of an endemic species of *Palaeopsylla* on that host in the mountains of Malaya, and another on Java. Since 85% of the 27 *Palaeopsylla* are Palaearctic, and the other 3 Oriental members of the genus are in South China, the Palaearctic origins of these fleas seem as clear as those of their hosts.

2. Erinaceids and Their Fleas

There are 2 members of the Erinaceidae that are found in parts of the Insular Malayan Area, namely the *Echinosorex* Blainville, 1838, the moonrat or gymnure and *Hylomys* Müller, 1839, the lesser gymnure. Both are monotypic and are present in Malaya and Borneo. The northern limit of *Echinosorex* is southern Thailand, and it is also found on Sumatra. *Hylomys* ranges throughout much of the Oriental mainland of Southeast Asia, and occurs on Sumatra and Java as well. So far as I am aware, there are no records of fleas from *Echinosorex*, nor from mainland *Hylomys*. A leptopsyllid, *Cratynius*, has been collected from *Hylomys* on Java (1 species) and Sabah, on Mt Kinabalu (2 species, both from the same locality). It is unusual for 2 species of fleas of a single genus to be found on the same species of host in one area, particularly a monotypic one with no local related taxa. As reported by Hopkins & Traub (1955), both Bornean species of *Cratynius* were very difficult to collect. Only 13 specimens are extant, even though 46 individuals of the presumed host, *Hylomys*, were examined carefully for fleas. Since 85% of the known specimens are from *Hylomys*, and since hundreds of other mammals in the same local area were checked to little or no avail, *Hylomys* nevertheless does seem to be the characteristic host, particularly since it is also associated with *Cratynius* on Java. Still, it is pointed out that recent collections of *Cratynius* on Java include specimens from the subgenus *Rattus*. Moreover, very few such commensal rats or wild forms of (*Rattus*) were examined by us on Mt Kinabalu. The absence of records of *Cratynius* from the mainland may represent inadequate collecting of *Hylomys*, for we have searched thousands of *R.* (*Rattus*) in various habitats in Malaya. There are not many species of leptopsyllids which infest insectivores, although a *Leptopsylla* from the Soviet Union is supposed to parasitize a shrew, and further study may disclose *Cratynius* is a murid-flea after all, like so many of its relatives.

Another unusual feature is that Leptopsyllidae are unknown in Malaya and are poorly represented in the Insular Malayan Area, although occurring on rats there, as previously noted. *Cratynius* is in the Leptopsyllinae, although it is placed in a distinctive tribe. While an endemic taxon, its roots are definitely Palaearctic, as indicated above, whether or not it is a true insectivore-flea.

G. Fleas and Their Hosts in the Insular Malayan Area

It has been shown above that except for the pygiopsyllids, virtually all of the fleas in the Malayan Subregion are clearly of Palaearctic origin, and the same is apparently true for, at least, the non-murid rodent-hosts. However, the data also have bearing on the apparent route of entry into the various parts of the Insular Malayan Area of both fleas and hosts, as well as upon certain features of the history of the fauna therein.

1. Zoogeographic Inter-Relationships of Malaya, Sarawak, and Sabah

Although Malaya and Borneo share a significant sciurid and murid fauna, the features in common are more notable for Malaya and Sarawak than Malaya and Sabah, and there appear to be some notable differences between the rodents and fleas of Sabah and those of Sarawak. Borneo may also have a somewhat closer faunal affinity with Malaya (and Sumatra) than with Java, while there is little to suggest any major entry into Borneo from Indo-China. Data bearing on these points may be summarized as follows.

Fifty per cent of the genera and 36% of the species of squirrels reported for either Malaya or Borneo occur in both areas. The comparable figures for murids are 43% and 41% respectively. The relationship is even more marked, for sibling species are also present, and some of the Malayan taxa reach their southern limits in that country. Of the species or species-groups treated in Table 2 (p. 398), 40% of the taxa of squirrels and 59% of the non-commensal murids occur in Malaya, Sarawak and Sabah. However, 3 of the rodents (9% of the total) are limited to Malaya and Sarawak, while 19% of the Bornean murids are found only in Sabah. One of the 18 species of Bornean squirrels is limited to Sarawak, and another is essentially so. All of the rodents common to Sabah and Malaya are likewise found in Sarawak. Relatively few of the mammals treated are shared by Indo-China and Borneo, and the exceptions (*Tupaia glis*, *Crocidura*, *Hylomys suillus* and *Rattus* (*Maxomys*) *fulvescens*) are wide-ranging and are found in Malaya as well.

Moreover, similar conclusions may be drawn from the records on fleas, particularly as summarized in Tables 11 and 12 (pp. 416 and 417). Thus, 3 species of *Medwayella* are common to Malaya and Sarawak but none of these are found in Sabah. (One, *M. robinsoni*, is found in Java, Sumatra and Thailand as well.) Only 12·5% of the 18 species of Sabah fleas (representing 10 genera) are known from Sarawak, while 88% of the 8 Sarawak fleas belong to *Medwayella*. The differences in the Sarawak and Sabah Siphonapteran fauna may reflect lack of adequate data from Sarawak, especially in the mountains, but the degree of diversity imply a definite zoogeographic phenomenon.

Ninety per cent of the 10 Malayan genera of fleas treated in this article are known from Java (and the sole exception is a species of *Lentistivalius* which infests birds). There are only 2 genera in Java which are not represented in Malaya, and only 4 such in Borneo. Seventy per cent of the 10 genera reported for Borneo are found in Malaya. There is also significant similarity at the species level. Malaya (with a total of 17 relevant species) and Java (with 15) share 5 species, representing 4 genera. Two of these are in *Medwayella*. Moreover, at least 3 of the other Malayan species

are closely allied to the Javanese. There is a minimum of 5 Bornean species of fleas which are near relatives of Malayan fleas.

Malaya and Java share 3 genera which are absent from Borneo, and all are of Palaearctic affinity. The 3 Bornean genera which are unknown in Java are all pygiopsyllids and hence with presumed ancestry in the Australian Region. Three of the genera unreported from Malaya are such pygiopsyllids.

None of the species of fleas we have been discussing are shared between Indo-China and Borneo. What relationships there are occur, at best, at the generic level, and lead to Malaya, and to a lesser extent, to Java and Sumatra. There are only 3 species common to both Indo-China and Malaya, belonging to 3 genera (*Stivalius s. lat.*, *Neopsylla* and *Macrostylophora*).

The data on both mammals and fleas, then, suggest that there is a significant degree of difference between the fauna of Sabah and Sarawak, and that the former tends more towards endemicity than the latter. It also appears that Sarawak shares more with Malaya than Sabah. Since so many elements of the Sabah fauna are apparently of Palaearctic ancestry, but with no real links with Indo-China, it seems that these probably entered Sabah from the south or southwest, originating from Malaya or Java or Sumatra, and did not penetrate from the north, from Indo-China or Formosa. Except for wide-ranging taxa, like *Callosciurus* and *Macrostylophora*, or *Neopsylla* (which occur throughout the intermediate areas), there is little in common in the pertinent fauna of Borneo on the one hand, and Indo-China and Formosa on the other. However, there is the notable case of the new species of Bornean *Macrostylophora* ex *Dremomys* on Mt Kinabalu, which also is known from Formosa (as a distinct subspecies). Nevertheless, *Dremomys* does occur over much of the Oriental Mainland of Southeast Asia (although not reported from Java or Sumatra). At our current level of knowledge, it is impossible to determine what such a distribution means, although it is this sort of circumstance that accounts for my regarding the foothills and lowlands of Formosa as belonging to the Oriental Region.

2. The Relative Poverty of the Javanese Mammalian Fauna

A glance at Table 10 (p. 415) discloses that many of the mammalian hosts listed for Malaya, Sumatra and Borneo are unrecorded from Java. Thus, of the 19 species or groups listed for Malaya, Sumatra and Borneo, only 8 (42%) are likewise represented on Java. The comparative sparsity of the Javanese mammalian fauna is well known. For example, Taylor (1934, pp. 98–99) stated: '. . . while *Ptilocercus*, *Dendrogale* and *Tana* [now placed in *Tupaia*—R.T.] are present in Borneo and Sumatra . . ., they appear to be totally wanting in Java. It suggests that Java was separated prior to the separation between Borneo and Sumatra or Borneo and the Asian Mainland'. Dammerman (1929) discusses the distribution of various mammals in these islands, as does Darlington (1957), mainly concerning the larger species. No doubt, extinctions have played an important part in the anomalous distribution, e.g. orangs and bears were present in Java during the Pleistocene but are absent today. The fauna of sciurids and rodents nevertheless seems disproportionately impoverished, and it is difficult to explain the absence of certain wide-

spread forms by extinctions of certain elements alone. It seems clear that Java must have had a different geological history than Sumatra or Borneo. It appears likely that subsidence of vast areas in the sea, coupled with enormous volcanic action over a large area, may have resulted in mass extinctions, and that only certain elements of the fauna of the Malayan Subregion could effect entry or re-entry thereafter. There is a good correlation in the taxa of Siphonaptera between Java and Borneo or Malaya, as noted above, but in view of the dearth of data from Sumatra, definitive interpretation is impossible.

3. Zoogeographic Inter-Relationships of Borneo and the Philippines

The data on the Philippines also provide evidence of the movement of the Oriental elements of Palaearctic ancestry via the Southeast Asian mainland through Indonesia and Borneo, as well as for the view that pygiopsyllids and certain murids had their ancestry in the Australian Region. A detailed consideration of these points, including the zoogeography of Luzon, will be presented elsewhere (Traub, in prep.) but the main features concerning these islands of the Philippines which are in the Malayan Subregion may be summarized as follows. A main route of entry from Borneo into the Philippines has been via the Palawan–Calamian groups of islands. Dickerson (1928, p. 26) regarded these islands as 'faunally . . . a northern extension of Borneo'. Taylor (1934) listed a number of Oriental and Palaearctic genera of mammals as occurring in the Palawan group, including such forms as tree-squirrels, flying-squirrels, *Tupaia*, scaly anteaters, badgers, mouse-deer, etc. He also wrote (p. 60) of 'direct migration from the mainland of Borneo, via land bridges at a time when Palawan and the Calamians were a peninsula of the island'. While I am not necessarily ascribing to the land-bridge theory rather than island-hopping as a means of travel, our data firmly support the main contentions of entry from Borneo to Palawan. For example, in the Palawan area are found a new species of *Medwayella* near *M. robinsoni*; the same new species of *Stivalius* near *S. jacobsoni* known from Borneo, and a new *Macrostylophora*, all on appropriate hosts. Another route from Borneo to the Philippines seems to have been from southeastern Sabah via the Tawitawi and Samales groups of small islands and Basilan Island. Here again Taylor speaks of a peninsula, but regardless of this point, the faunal connections are clear. Mindanao and the adjacent islands have a mammalian and Siphonapteran fauna that is distinct from that of Palawan in major respects, but a large component is of Bornean origin. For example, the flying-squirrel *Petinomys* Thomas, 1908, which is known from Ceylon, South India, Burma, South China, Malaya, Sumatra and Borneo, is also found on Basilan Island, but apparently nowhere else in the Philippines. On the other hand, *Hylopetes*, a flying-squirrel of the Eastern Palaearctic Region which also occurs in the mountains of the Malayan Subregion, including Borneo, is found in the Palawan area but not elsewhere in the Philippines. Similarly, the hyosciurine *Nannosciurus* (Callosciurini), known from 1 species in Sabah, is represented by separate species on Basilan Island, and Samar, and 2 on Mindanao, but not the Palawan area.

However, unlike Palawan, Mindanao shares faunal elements, or at least a heritage,

with Celebes and New Guinea. Members of the murid subfamily Hydromyinae are known only from Australia, New Guinea and the Philippines, and, indeed, Simpson (1961) suggested that two endemic genera in the Philippines (Luzon and/or Mindanao) came from New Guinean stock (although ultimately derived from Asian forebears). Huge, specialized tree-rats occur in Celebes, Ceram, New Guinea and the Philippines, although it is difficult to say how closely these are related to one another. The subfamily Phloeomyinae, which Simpson recognized in 1945, includes some of these tree-rats in the four areas and is unknown elsewhere, unless the Oriental *Chiropodomys* Peters, 1868, is placed therein. Actually, in 1961 Simpson apparently had doubts about the validity of the subfamily, for he did not refer to the name, but Anderson & Jones (1967), Cockrum (1962) and others still use Simpson's 1945 scheme of classification. Misonne (1969) likewise did not utilize the name Phloeomyinae but concurred that the genera which Tate (1936) placed here are related. Most of the murid-fleas of Mindanao are pygiopsyllids, and 2 of the 5 known genera there have definite affinities with representatives in Celebes and New Guinea.

4. Some Unusual Features about the Distribution of Callosciurine Fleas

There are several anomalous features about the distribution of the fleas associated with certain of the callosciurines under discussion. For example, although some of the same species of squirrels, such as *Callosciurus notatus* and *C. nigrovittatus*, are found from Malaya to Sabah, they are infested with very different fleas in Sabah than in Malaya, or even Sarawak. Before discussing this further, it is necessary to consider some general points about the distribution of fleas and their hosts. Certain species of fleas are found throughout the ranges of their hosts, e.g. the ceratophyllid *Orchopeas leucopus* (Baker, 1904) on *Peromyscus maniculatus* (Wagner, 1845), from eastern Canada to deep into Mexico, the Rocky Mountain area and California; *O. howardi* (Baker, 1895) on *Sciurus caroliniensis* Gmelin, 1788, all over the eastern U.S.A. to Texas. Sometimes the range of the flea extends beyond that of one host, occurring on closely related species, such as *O. howardi* on other *Sciurus* Linnaeus, 1758, all the way to southern Mexico. There are some species of fleas which fairly indiscriminately infest members of a tribe or subfamily, such as *Malaraeus penicilliger* (Grube, 1852)[12] on various voles, from northern Europe, Asia (including the high Himalayas) and Alaska; or the Holarctic *Tarsopsylla octodecimdentata* on sundry Sciurinae. In other instances the relationship seems to be between the genus of flea and the genus of host, e.g. the doratopsylline *Corrodopsylla* Wagner, 1929, on *Sorex* Linnaeus, 1758, from Europe and Japan, and Alaska to at least central Mexico. On the other hand, there are surprising examples of marked speciation of fleas infesting presumably monotypic genera of mammals, where the hosts are geographically restricted to relatively small areas and within which there are no overt factors of contemporary isolation, e.g. 4 species of *Astivalius* Smit, 1953, on

[12] A variety of subspecies of *M. penicilliger* have been named, and some of these apparently represent distinct species, but the point still holds.

Lorentzimys nouhuysi Jentink, 1911, in New Guinea and at least 5 species of *Phaenopsylla* Jordan, 1944, on *Calomyscus bailwardi* Thomas, 1905, in the deserts of Soviet Central Asia, Iran, Afghanistan and West Pakistan.

In the case of the *Callosciurus* cited above, *Medwayella robinsoni* is the characteristic flea in Thailand, Malaya, Sumatra, Java and Sarawak, but on Mt Kinabalu these are infested with *Macrostylophora* in the absence of *Medwayella*. Moreover, in Malaya, *Macrostylophora* is not associated with these particular squirrels. It may be that at 5500–6500 ft elevation, where these *Callosciurus* were examined for fleas on Mt Kinabalu, the climate is too temperate for *Medwayella*, for no members of the genus have been found there, although they are present on the mountain at about 2000 ft elevation. The genus is rare at height of 6000 ft in Malaya.

The unusual host-specificity noted for the *Macrostylophora* on *C. notatus* and *C. nigrovittatus* on Mt Kinabalu is also worth emphasis. Even squirrels on the same trees did not share fleas. Such specificity is unusual in *Macrostylophora*, at least on the Asian mainland, where *M. hastata* has been found on several species of *Callosciurus* and on *Tamiops* Allen, 1906. *M liae* is also found on those 2 genera of squirrels.

IV. CONCLUSIONS

1. Fleas of the family Pygiopsyllidae originated in the Australian Region and from there moved north and west through the Malfilindo Archipelagoes to the mainland of Asia.

2. While the Siphonapteran genus *Medwayella* has its roots in the Australian Region, it apparently arose in the Malayan Subregion, probably in Borneo, where it is best represented.

3. *Medwayella* is a relatively youthful and specialized taxon, whose true hosts are squirrels of the tribe Callosciurini, and not tupaiids (tree-shrews), and its characteristic habitat is in the foothills and lower elevations of the mountains of the Malayan Subregion and parts of the Burmo-Chinese Subregion.

4. With the exception of the pygiopsyllids *Medwayella* and *Lentistivalius*, the fleas of squirrels of the Oriental Region have definite Palaearctic affinities, as do those of the tree-squirrels of the Ethiopian Region.

5. The callosciurines of the Insular Malayan Area and Wallacea are, geologically speaking, relatively recent emigrants from the mainland of the Malayan Subregion, which penetrated to Borneo via Sumatra and/or Java, and thence to the Philippines and Celebes, carrying their ceratophyllid fleas with them, at least as far as Palawan and Mindanao.

6. *Medwayella*, however, moved in the opposite direction, from Borneo to the mainland and as far as Indo-China, but also emigrated to the Philippines.

7. While the available evidence cannot rule out that the Sciuridae originated in the 'Old World Tropics', the data suggest the possibility that the Oriental members (or at least the Petauristinae) had Palaearctic roots and that their forebears penetrated into and radiated within the Oriental Region.

8. Regardless of the point of origin of the ancestors of the genus *Rattus* (which

may have been in the Australian Region), the members of the genus and especially the subgenus *Rattus*, are relatively youthful, and worked their way back and forth between the mainland and the Australo-Asian Archipelagoes. In the process they transported from the west and northwest, certain fleas of Palaearctic stocks. At least one of these (*Sigmactenus*) has reached as far east as New Guinea.

9. *Stivalius s. str.*, although descended from fleas of the Australian Region, has been intimately associated with the subgenus *Rattus* (especially *R.* (*R.*) *rattus*), and like *Xenopsylla* of the *X. vexabilis*-group, has accompanied these rats on many of their peregrinations.

10. The insectivores and their fleas in the Insular Malayan Area are likewise of Palaearctic ancestry and entered the islands from the Malayan peninsula.

11. The data on Siphonaptera of squirrels, rats and insectivores therefore are in accord with certain, but not all, of the contentions of Darlington (1957), Simpson (1961) and others, who believe that the mammals of the Australo-Asian Archipelagoes were derived from the Asian mainland, and that the genus *Rattus* was a late emigrant.

12. Nevertheless, study of the Siphonaptera also provide strong evidence that, contrary to the belief of virtually all mammalogists, there were ancient faunal connections, involving mammals, between the Southern Continents (albeit tenuous and transient ones, via island-hopping) and hence provide support for the theory of Continental Drift.

13. Malaya, Sumatra, Java and Borneo share many faunal features, but there are significant differences between the mammals and fleas of Sarawak and those of Sabah, with the former resembling Malaya more than does the latter.

14. Although certain species of squirrels range from Thailand to Sabah, and are infested with *Medwayella robinsoni* as far east as Sarawak, they carry different fleas in Sabah (i.e. *Macrostylophora*) and these are highly host-specific there.

15. Palawan and Mindanao have derived much of their relevant fauna from Borneo, but Mindanao also has elements of Wallacean and New Guinean stocks.

V. SOURCES

In dealing with the nomenclature and classification of mammalian hosts, a certain amount of confusion is inevitable. The scheme of classification that has received global recognition is that of Simpson (1945), and the fact that general texts on mammals even as much as 20 years later, such as Cockrum (1962), Anderson & Jones (1967), Morris (1965) and Walker et al. (1968) all follow Simpson's system demonstrate how sound and useful it was. However, parts of the classification are out of date, as indicated above, and where it was pointed out that Simpson in 1961 did not fully adhere to his 1945 format when dealing with murids. Unfortunately, there has been no general opus with an alternate, complete plan of classification and there are differences of opinion expressed amongst specialists dealing with sundry components. Another problem is due to the enormous taxonomic difficulties posed by the murids, and even Misonne (1969) in his large work on rats did not indicate precisely to which subgenus certain rats (e.g. *R. baluensis*) belong.

Accordingly, we have had to rely upon several authorities for the names and

taxonomic status of the mammals mentioned in this article. The basic system of classification is that of Simpson (1945), as used by Anderson & Jones (1967), etc. For Bornean mammals, we have followed Medway (1963) and for Malayan, Harrison (1966). As applicable, and when not in conflict with the above, we have also used Ellerman & Morrison-Scott (1951) for Palaearctic taxa and Laurie & Hill (1954) for the New Guinean and Wallacean ones. In specific instances we have used the names employed by Misonne (1969) on the basis of 'latest reviser' and obvious merit, but in those cases, these have been indicated. Other exceptions have also been noted in the text.

The basic classification of Siphonaptera at the higher levels is essentially that of Hopkins & Rothschild (1962 and 1966), but since the Pygiopsyllidae, Ceratophyllidae and some other critical taxa have not yet been treated by these authorities, I have used my own ideas, down to the species and subspecies. The data presented include genera and species new to Science, since these amount to an equivalent of a minimum of 5% of the known fauna, and a much higher figure for the zoogeographic areas in question.

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Aenigmopsylla Ioff, 1950
Astivalius Smit, 1953
Brevictenidia Liu & Li, 1965
Callopsylla Wagner, 1934
Ceratophyllus Curtis, 1832
Citellophilus Wagner, 1934
Conorhinopsylla Stewart, 1927
Corrodopsylla Wagner, 1929
Cratynius Jordan, 1933
Cratynius audyi (Traub, 1952)
Cratynius bartelsi Jordan, 1933
Cratynius crypticus Hopkins & Traub, 1955
Dasypsyllus gallinulae (Dale, 1878)
Dasypsyllus stejnegeri (Jordan, 1929)
Echidnophaga Olliff, 1886
Epitedia Jordan, 1938
Frontopsylla Wagner & Ioff, 1926
Frontopsylla (*F.*) *nakagawai* Kumada & Sakaguti, 1959
Gryphopsylla Traub, 1957
Gryphopsylla hopkinsi (Traub, 1957)
Hollandipsylla Traub, 1953
Hollandipsylla neali Traub, 1953
Kohlsia Traub, 1950
Lentistivalius Traub, 1972
Lentistivalius ferinus (Rothschild, 1908)
Lentistivalius insolli (Traub, 1950)
Lentistivalius vomerus Traub, 1972
Leptopsylla Jordan & Rothschild, 1911
Leptopsylla (*Pectinoctenus*) Wagner, 1928
Libyastus Jordan, 1936
Macrostylophora Ewing, 1929
Macrostylophora borneensis (Jordan, 1926)
Macrostylophora cuiae Liu, Wu & Yu, 1964
Macrostylophora euteles (Jordan & Rothschild, 1911)
Macrostylophora exilia Li, Wang & Hsieh, 1964
Macrostylophora fimbriata (Jordan & Rothschild, 1921)
Macrostylophora hastata (Jordan & Rothschild, 1921)
Macrostylophora heinrichi Jordan, 1939
Macrostylophora idoneus (Rothschild, 1919)
Macrostylophora levis (Jordan & Rothschild, 1922)
Macrostylophora liae Wang, 1957
Macrostylophora lupata (Jordan & Rothschild, 1921)
Macrostylophora phillipsi (Jordan, 1925)
Macrostylophora pilata (Jordan & Rothschild, 1922)
Macrostylophora probata (Jordan & Rothschild, 1922)
Macrostylophora sodalis (Rothschild, 1919)
Macrostylophora trispinosa (Liu, 1939)
Macrostylophora uncinalis Jordan, 1939
Malaraeus penicilliger (Grube, 1852)
Medwayella Traub, 1972
Medwayella angustata Traub, 1972
Medwayella arcuata Traub, 1972
Medwayella batibacula Traub, 1972
Medwayella calcarata Traub, 1972
Medwayella dryadosa Traub, 1972
Medwayella javana (Jordan, 1933)
Medwayella limi Traub, 1972
Medwayella loncha (Jordan, 1926)
Medwayella phangi Traub, 1972
Medwayella rhaeba (Jordan, 1926)
Medwayella robinsoni (Rothschild, 1905)
Medwayella thurmani Traub, 1972
Medwayella veruta Traub, 1972
Megarthroglossus Jordan & Rothschild, 1915
Metastivalius Holland, 1969
Monopsyllus Kolenati, 1857
Monopsyllus anisus (Rothschild, 1907)
Monopsyllus argus (Rothschild, 1908)
Monopsyllus tolli (Wagner, 1901)
Neopsylla Wagner, 1903
Neopsylla avida Jordan, 1931
Neopsylla dispar Jordan, 1932
Neopsylla luma Traub, 1954
Neopsylla setosa (Wagner, 1898)
Neopsylla sondaica Jordan, 1931
Neopsylla stevensi Rothschild, 1915
Neopsylla tricata Jordan, 1931
Nosopsyllus Jordan, 1933
Nosopsyllus fasciatus (Bosc., 1801)
Nosopsyllus londiniensis (Rothschild, 1903)
Opisodasys Jordan, 1933
Opisodasys pseudarctomys (Baker, 1904)
Opisodasys vesperalis (Jordan, 1929)
Orchopeas Jordan, 1933
Orchopeas bolivari Barrera, 1955
Orchopeas howardi (Baker, 1895)
Orchopeas leucopus (Baker, 1904)
Palaeopsylla Wagner, 1903
Palaeopsylla apsidata Traub & Evans, 1967
Palaeopsylla laxata Jordan, 1933
Paraceras Wagner, 1916
Paraceras crispis (Jordan & Rothschild, 1911)
Paraceras hamatum Jordan, 1939
Paraceras javanicum (Ewing, 1924)

Paraceras melinum (Jordan, 1925)
Paraceras melis (Walker, 1856)
Paraceras pendleburyi Jordan, 1932
Paraceras sauteri (Rothschild, 1914)
Peromyscopsylla L. Fox, 1939
Peromyscopsylla himalaica (Rothschild, 1915)
Phaenopsylla Jordan, 1944
Pleochaetis Jordan, 1933
Pleochaetis dolens quitanus (Jordan, 1931)
Pygiopsylla Rothschild, 1906
Pygiopsylla tiptoni Traub, 1957
Rhadinopsylla Jordan & Rothschild, 1912
Rhadinopsylla (*Rectofrontia*) *japonica* Sakaguti & Jameson, 1956
Rothschildiana Smith, 1952
Rothschildiana kopsteini (Jordan, 1931)
Rothschildiana smiti Traub, 1957
Sigmactenus Traub, 1950
Sigmactenus alticola Traub, 1954
Sigmactenus toxopeusi Smit, 1953
Sigmactenus werneri Traub, 1950
Stenischia Jordan, 1932
Stivalius Jordan & Rothschild, 1922
Stivalius aporus Jordan & Rothschild, 1922
Stivalius celebensis (Ewing, 1924)
Stivalius cognatus Jordan & Rothschild, 1922
Stivalius jacobsoni (Jordan & Rothschild, 1922)
Stivalius klossi (Jordan & Rothschild, 1922)
Stivalius mjoebergi Jordan, 1926
Stivalius pomerantzi Traub, 1951
Syngenopsyllus Traub, 1950
Syngenopsyllus calceatus (Rothschild, 1905)
Tarsopsylla Wagner, 1927
Tarsopsylla octodecimdentata (Kolenati, 1863)
Xenopsylla Glinkiewicz, 1907
Xenopsylla cheopis (Rothschild, 1903)
Xenopsylla nesiotes (Jordan & Rothschild, 1908)
Xenopsylla papuensis (Jordan, 1933)
Xenopsylla vexabilis Jordan, 1925

IX. LIST OF MAMMALS CITED IN TEXT

Anathana Lyon, 1913
Anathana ellioti (Waterhouse, 1850)
Apodemus Kaup, 1829
Bandicota Gray, 1873
Bandicota bengalensis (Gray & Hardwicke, 1833)
Bandicota indica (Bechstein, 1800)
Callosciurus Gray, 1867
Callosciurus albescens (Bonhote, 1901)
Callosciurus caniceps (Gray, 1842)
Callosciurus erythraeus (Pallas, 1779)
Callosciurus hippurus (Geoffroy, 1832)
Callosciurus nigrovittatus (Horsfield, 1824)
Callosciurus notatus (Boddaert, 1785)
Callosciurus prevosti (Desmarest, 1822)
Calomyscus Thomas, 1905
Calomyscus bailwardi Thomas, 1905
Chimarrogale Anderson, 1877
Chiropodomys Peters, 1868
Chiropodomys gliroides (Blyth, 1856)
Chiropodomys major Thomas, 1893
Chiropodomys muroides Medway, 1963
Crocidura Wagler, 1832
Dendrogale Gray, 1848
Dendrogale melanura (Thomas, 1892)
Dendrogale murina (Schlegel & Müller, 1845)
Dremomys Heude, 1898
Dremomys everetti (Thomas, 1890)
Dremomys rufigenis (Blanford, 1878)
Echinosorex Blainville, 1838
Echinosorex gymnurus (Raffles, 1821)
Exilisciurus Moore, 1958
Exilisciurus exilis (Müller, 1838)
Exilisciurus whiteheadi (Thomas, 1887)
Funambulus Lesson, 1835
Glyphotes Thomas, 1898
Glyphotes (*G.*) *simus* Thomas, 1898
Glyphotes (*Hessonoglyphotes*) *canalvus* Moore, 1959
Haeromys Thomas, 1911
Haeromys margarettae (Thomas, 1893)
Haeromys pusillus (Thomas, 1893)
Hapalomys Blyth, 1859
Hapalomys longicaudatus Blyth, 1859
Hylomys Müller, 1839
Hylomys suillus Müller, 1839
Hylopetes Thomas, 1908
Lariscus (*L.*) *insignis* (F. Cuvier, 1821)
Lariscus (*Paralariscus*) *hosei* (Thomas, 1892)
Lorentzimys nouhuysi Jentink, 1911
Melogale (*Helictis*) Gray, 1831
Melogale (*Helictis*) *orientalis everetti* (Thomas, 1895)
Menetes Thomas, 1908
Menetes berdmorei (Blyth, 1849)
Mus musculus Linnaeus, 1758
Nannosciurus Trouessart, 1880
Nannosciurus melanotis (Müller, 1838)

Neotoma Say & Ord, 1825
Ochotona Link, 1795
Oryzomys Baird, 1857
Peromyscus Gloger, 1841
Peromyscus maniculatus (Wagner, 1845)
Petaurista Link, 1795
Petinomys Thomas, 1908
Pithecheir Cuvier, 1838
Pithecheir melanurus Cuvier, 1838
Pogonomys Milne-Edwards, 1877
Prosciurillus Ellerman, 1947
Ptilocercus Gray, 1848
Ptilocercus lowi Gray, 1848
Rattus Fischer, 1803
Rattys (*Berylmys*) Ellerman, 1947
Rattus (*Bullimus*) Mearns, 1905
Rattus (*Bullimus*) *berdmorei* (Blyth, 1851)
Rattus (*Bullimus*) *xanthurus* (Gray, 1867)
Rattus (*Lenothrix*) Miller, 1903
Rattus (*Lenothrix*) *alticola* (Thomas, 1888)
Rattus (*Lenothrix*) *baeodon* (Thomas, 1894)
Rattus (*Lenothrix*) *canus* (Miller, 1903)
Rattus (*Lenothrix*) *inas* Bonhote, 1906
Rattus (*Lenothrix*) *ochraceiventer* (Thomas, 1894)
Rattus (*Lenothrix*) *rajah* (Thomas, 1894)
Rattus (*Lenothrix*) *surifer* (Miller, 1900)
Rattus (*Lenothrix*) *whiteheadi* (Thomas, 1894)
Rattus (*Leopoldamys*) *edwardsi* (Thomas, 1882)
Rattus (*Leopoldamys*) *sabanus* (Thomas, 1887)
Rattus (*Maxomys*) Sody, 1936
Rattus (*Maxomys*) *cremoriventer* (Miller, 1900)
Rattus (*Maxomys*) *fulvescens* (Gray, 1847)
Rattus (*Maxomys*) *niviventer* (Hodgson, 1836)
Rattus (*Rattus*) Fischer, 1803
Rattus (*Rattus*) *annandalei* (Bonhote, 1903)
Rattus (*Rattus*) *argentiventer* (Robinson & Kloss, 1916)
Rattus (*Rattus*) *baluensis* (Thomas, 1894)
Rattus (*Rattus*) *exulans* (Peale, 1848)
Rattus (*Rattus*) *norvegicus* (Berkenhout, 1769)
Rattus (*Rattus*) *rattus* (Linnaeus, 1758)
Rattus (*Rattus*) *tiomanicus* (Miller, 1900)
Rattus (*Stenomys*) *bowersi* (Anderson, 1879)
Rattus (*Stenomys*) *infraluteus* (Thomas, 1888)
Rattus (*Stenomys*) *muelleri* (Jentink, 1879)
Ratufa Gray, 1867
Ratufa affinis (Raffles, 1822)
Rheithrosciurus Gray, 1867
Rheithrosciurus macrotis (Gray, 1856)
Rhinosciurus Gray, 1843
Rhinosciurus laticaudatus (Müller, 1844)
Sciurus Linnaeus, 1758
Sciurus caroliniensis Gmelin, 1788
Sorex Linnaeus, 1758
Suncus Ehrenberg, 1833
Sundasciurus Moore, 1958
Sundasciurus (*S.*) *brookei* (Thomas, 1892)
Sundasciurus (*Aletesciurus*) *hippurus* (Geoffroy, 1832)
Sundasciurus (*S.*) *jentinki* (Thomas, 1887)
Sundasciurus (*S.*) *lowi* (Thomas, 1892)
Sundasciurus (*S.*) *tenuis* (Horsfield, 1824)
Tamiops Allen, 1906
Tamiops macclellandi (Horsfield, 1839)
Tamiops swinhoei (Milne-Edwards, 1874)
Tana Lyon, 1913
Thomasomys Coues, 1884
Tupaia Raffles, 1821
Tupaia dorsalis Schlegel, 1857
Tupaia glis (Diard, 1820)
Tupaia gracilis Thomas, 1893
Tupaia javanica Horsfield, 1821
Tupaia minor Günther, 1876
Tupaia montana Thomas, 1892
Tupaia nicobarica (Zelebor, 1869)
Tupaia picta Thomas, 1892
Tupaia splendidula Gray, 1865
Tupaia tana Raffles, 1821
Urogale Mearns, 1905
Urogale everetti (Thomas, 1892)
Xerus Ehrenberg, 1833

X. LIST OF TABLES

TABLE 5 Distribution of species of genera of fleas which have representatives infesting squirrels in the Malayan and South-eastern Oriental Subregions.

TABLE 6 Major fleas of tree-squirrels (Nos 1–5), scansorial squirrels (Nos 7–8) and ground-squirrels in certain areas of the Oriental Region.

TABLE 7 Major fleas of tree-shrews (tupaiids) (Nos 1–2), rats (Nos 3–10) and insectivores in certain areas of the Oriental Region.

TABLE 8 Genera of Siphonaptera with species infesting arboreal or scansorial squirrels.

TABLE 9 Distribution of fleas of arboreal and semi-arboreal squirrels, i.e. excluding fleas of chipmunks, spermophiles, etc., with total numbers of genera and species per constituent families. (Fleas of volant hosts deleted.)

TABLE 10 Distribution of certain mammals in Malaya, Sumatra, Java and Borneo.

TABLE 11 Species of fleas of non-volant hosts known from Malaya, Java, Sarawak and Sabah. (Wide-ranging fleas of commensals excluded.)

TABLE 12 Numbers of genera of fleas shared by Malaya, Java or Borneo (Sabah and Sarawak only), with names and zoogeographic (regional) affinities of absentees. (Fleas of non-volant hosts.) (Wide-ranging fleas of commensals excluded.)

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